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**Updated (2003–2015) Biological Synopsis of Grass Carp
(*Ctenopharyngodon idella*)**

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

Grass Carp (*Ctenopharyngodon idella*) has been introduced worldwide from its native range in Eastern Asia. This species was first introduced in the United States in the early 1960s and has since established reproducing populations in several major rivers of the United States. Impacts associated with Grass Carp introductions include changes to aquatic vegetation and habitat, community structure and processes, and water quality. Given its potential to invade Canadian watersheds via waterways connected to the Mississippi River basin, live trade, or other pathways, there is considerable concern for their potential ecological impacts if introduced to Canada. Using information on Grass Carp biology, a risk assessment conducted by Fisheries and Oceans Canada (DFO) in 2004 identified Grass Carp to be a high ecological risk to Canada if introduced. Such risk assessments need to be adaptive, taking into account new approaches and data. This biological synopsis is intended to update information on Grass Carp, specifically focusing on the literature published between 2003 and early 2015, and will be used to inform a binational Grass Carp risk assessment. Current knowledge on the distribution, taxonomy, ecology and impacts of Grass Carp are outlined in this report, and includes details on the longevity, physiological tolerance, diet, fecundity, adaptability, and dispersal potential of Grass Carp where it has been studied.

Mise à jour (2003–2015) du sommaire biologique de la carpe de roseau (*Ctenopharyngodon idella*)

RÉSUMÉ

La carpe de roseau (*Ctenopharyngodon idella*) s'est répandue sur tout le globe depuis son aire de répartition indigène, dans l'est de l'Asie. Cette espèce a d'abord été introduite aux États-Unis au début des années 1960, puis de nombreuses populations se sont établies dans plusieurs cours d'eau importants au pays. Les impacts associés à l'introduction de la carpe de roseau comprennent notamment des changements dans la végétation aquatique et l'habitat, la structure et les processus des communautés, ainsi que la qualité de l'eau. Puisqu'il est fort possible que la carpe de roseau envahisse les eaux canadiennes en passant par des cours d'eau reliés au bassin du fleuve Mississippi, ou d'autres voies de passage, les impacts écologiques potentiels associés à son introduction au Canada suscitent de vives inquiétudes. Au moyen de renseignements sur la biologie de la carpe de roseau, une évaluation du risque menée en 2004 par Pêches et Océans Canada (MPO) a reconnu que cette espèce présentait un risque écologique élevé pour le Canada si elle y était introduite. De telles évaluations du risque doivent être adaptatives et tenir compte des nouvelles approches et données. Le présent sommaire biologique vise à mettre à jour l'information sur la carpe de roseau, en mettant l'accent sur les études publiées entre 2003 et le début de 2015, et il servira à documenter l'évaluation binationale du risque de la carpe de roseau. Les connaissances actuelles sur la répartition, la taxonomie, l'écologie et les impacts de la carpe de roseau sont présentées dans ce rapport, et comprennent des détails sur la longévité, la tolérance physiologique, le régime alimentaire, la fécondité, l'adaptabilité et le potentiel de dispersion de la carpe de roseau aux endroits où elle a été étudiée.

INTRODUCTION

Grass Carp (*Ctenopharyngodon idella*) is a freshwater fish species that has been extensively introduced worldwide, including to North America, primarily for use in the biological control of aquatic vegetation (Pípalová 2006, USGS 2015). Although sterile strains (i.e., triploid Grass Carp) are now often used, self-sustaining populations of diploid Grass Carp have escaped into North American waterbodies of close proximity to Canada (USGS 2015). Range expansion of established populations in the United States continues to occur, particularly in the Mississippi drainage basin. Given the invasion history, proximity to Canadian waters, and potential impact, the Grass Carp represents a serious ecological threat. A risk assessment completed in 2004 by the Fisheries and Oceans Canada (DFO) Centre of Expertise for Aquatic Risk Assessment (CEARA) identified the risk of Grass Carp survivorship, reproduction, and spread in Canada to be high with reasonable certainty, and it was very certain that the ecological consequences of establishment would be high for Canadian aquatic ecosystems (Mandrak and Cudmore 2004). Recent research on Grass Carp caught in the Lake Erie basin has increased concern of Grass Carp introduction to the Great Lakes, as analyses indicate they were produced through natural reproduction within the system (Chapman et al. 2013).

Considering the high risk associated with Grass Carp, it is imperative to maintain an accurate and detailed account of Grass Carp biology such that sound scientific advice on the ecological risk associated with a potential invasion in Canada can be delivered. This report provides an update to the previous biological synopsis of Grass Carp, which reviewed literature prior to 2003 (Cudmore and Mandrak 2004). Since 2003, a vast amount of Grass Carp research has been conducted. A substantial portion of this research focuses on Grass Carp aquaculture practices and associated issues (e.g., immune responses, processing and preservation for human consumption, optimal diet and rearing conditions); however, except as it applies to risk of introduction, this synopsis does not extend to cover this literature. A substantial portion of valuable information on Grass Carp also exists in the Chinese- and Russian-language literature; this literature, from 1940 to present, is reviewed and synthesized by Zhao and Wang (Chinese literature; Ontario Ministry of Natural Resources and Forestry [OMNRF] unpubl. report) and Bogutskaya et al. (Russian literature; 2017). This document is presented to provide up-to-date biological synopsis for use in the updated risk assessment of Grass Carp to Canada.

NAME AND CLASSIFICATION

From Froese and Pauly (2015), Global Invasive Species Database (2005), and Integrated Taxonomic Information System (2015):

Kingdom: Animalia

Phylum: Chordata

Class: Actinopterygii

Order: Cypriniformes

Family: Cyprinidae

Genus: *Ctenopharyngodon*

Species: *Ctenopharyngodon idella* Valenciennes, 1844

Grass Carp has been listed as part of the subfamily Squaliobarbinae (Nelson 2006, Froese and Pauly 2015), Oxygastrinae (Eschmeyer, 2014), or Leuciscinae (Ross 2001, Wang et al. 2008,

He et al. 2008); however, recent phylogenetic analyses indicate that there is strong evidence to support the placement of Grass Carp into the subfamily Oxygastrinae (Tang et al. 2013a, b).

Synonyms:

Ctenopharyngodon idella Valenciennes 1844

Ctenopharyngodon idella Valenciennes, 1844

Ctenopharyngodon idellos Valenciennes, 1844

Ctenopharyngodon idellus Valenciennes 1844

Ctenopharyngodon idellus Valenciennes, 1844

Ctenopharyngodon laticeps Steindachner, 1866

Leuciscus idella Valenciennes, 1844

Leuciscus idellus Valenciennes, 1844

Leuciscus tschiliensis Basilewsky, 1855

Pristiodon siemionovii Dybowski, 1877

Sarcocheilichthys teretiusculus Kner, 1867

Common English name: Grass Carp

Other English names: Chinese carp, gardd carp, silver orfe, white amur

Common French names: amour blanc, carpe amour, carpe de roseau, carpe herbivore, chinoise, China cardfish, Chinese buffalo

Common names for 37 other languages are listed on FishBase (Froese and Pauly 2015).

DESCRIPTION

Grass Carp (Figure 1) is a freshwater cyprinid and represents the only species of the genus *Ctenopharyngodon*, from the Greek word meaning "comb-like pharyngeal teeth". It is one of the largest cyprinid fishes in the minnow family (Cyprinidae) (Cudmore and Mandrak 2004), with a maximum recorded length of 150 cm and maximum published weight of 45 kg, and typically lives 5–11 years (Schofield et al. 2005).

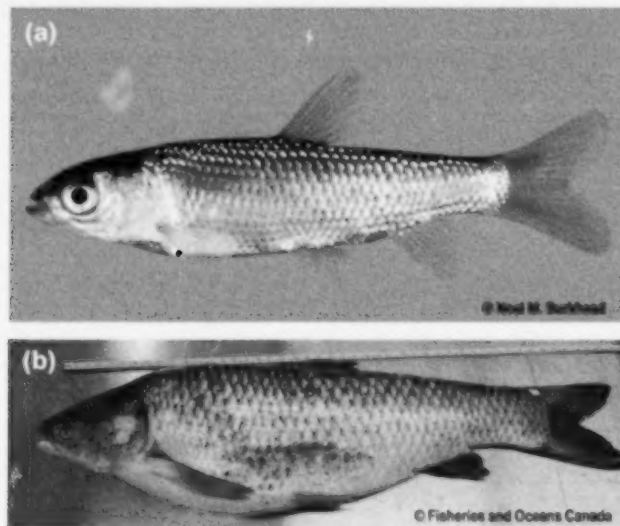


Figure 1. Photographs (not to scale) of (a) juvenile and (b) adult Grass Carp (*Ctenopharyngodon idella*).

Grass Carp has a large, elongated, laterally compressed body with a complete, slightly decurved lateral line and no ventral keel, and a wide, blunt, scaleless head with moderately small eyes, very short snout, and terminal mouth without teeth or barbels (Ross 2001, Cudmore and Mandrak 2004, Page and Burr 2011). The body is covered in large, dark-edged, cycloid scales (34–45 on lateral line) giving a cross-hatched appearance (Schofield et al. 2005, Page and Burr 2011). The caudal fin is forked and the dorsal fin origin is anterior to the pelvic fin origin (Schofield et al. 2005). There are 7–8 dorsal fin soft rays, 8–10 anal fin soft rays, and the paired pectoral fins have 15–20 soft rays (Ross 2001, Schofield et al. 2005). Dorsal and anal fins do not have spines and there is no adipose fin (Schofield et al. 2005, Page and Burr 2011). Pharyngeal teeth with strongly ridged grinding surfaces are in two rows and may count 2, 4–4, 2, 2.5–4, 2 or 2, 4–5, 2 (Schofield et al. 2005, Page and Burr 2011). The gill rakers are described as short, unfused, and widely set, and 12–16 on the first arch (Schofield et al. 2005).

Adult Grass Carp are often dark gray to brassy green along the dorsal surface, becoming lighter (silvery, white to yellow) on the sides and underbody (Ross 2001, Page and Burr 2011). The head is often uniform gray and is usually darker than the rest of the body. Fins are typically clear to green-gray to dull silver. At onset of maturity, and during the breeding season, external sexual dimorphism appears (Cudmore and Mandrak 2004). Males develop deciduous tubercles on the dorsal and medial surfaces of the pectoral fins. Females may also develop rough pectoral surfaces but they are not as highly developed as in the males. During breeding season, females exhibit soft, distended abdomens and swollen, pinkish vents.

Grass Carp eggs are non-adhesive and semi-buoyant (Cudmore and Mandrak 2004). Upon release, Grass Carp eggs are small (2.0–2.5 mm diameter) but swell as they absorb water until they reach a diameter of 5.0–6.0 mm (Cudmore and Mandrak 2004). In the native range, variation in Grass Carp egg diameter has been reported to range from 3.5 to 6.7 mm (Yi et al. 2006). Drifting eggs of native North American cyprinid species are generally smaller (Chapman and Wang 2006). In a study of embryonic and larval development in Grass Carp in the U.S., mean water hardened egg diameter ranged from 4.02 to 4.65 mm (George and Chapman 2015). The eyes of Grass Carp larvae are larger, more circular, and tend to be positioned more anteriorly in the head compared to many other native cyprinid and catostomid larvae of the Mississippi River basin (Chapman and Wang 2006). Unlike other riverine larvae from central

North America, Grass Carp larvae tend to have a prominent dark spot on the inner ventral aspect of each eye prior to complete pigmentation of the eye (Chapman and Wang 2006). Grass Carp larvae generally have 31–33 preanal and 10–12 postanal myomeres (Chapman and Wang 2006). A detailed review of morphology during early development is provided by Yi et al. (2006).

Grass Carp is superficially similar to several other fishes present in North America, such as large Creek Chub (*Semotilus atromaculatus*) and Bluehead Chub (*Nocomis leptoccephalus*), as well as the Goldfish (*Carassius auratus*), Common Carp (*Cyprinus carpio*), Black Carp (*Mylopharyngodon piceus*), Silver Carp (*Hypophthalmichthys molitrix*), and Bighead Carp (*Hypophthalmichthys nobilis*) (Ross 2001). The chubs have rounder heads and possess barbels; Goldfish and Common Carp have broader dorsal fins and have single stout spines in the dorsal and anal fins (Ross 2001, Page and Burr 2011). Common Carp also has barbels on each side of the mouth and Goldfish lack dark-edged scales characteristic of Grass Carp (Page and Burr 2011). Grass Carp adults can be distinguished from Black Carp by the morphology of pharyngeal teeth and body color (Black Carp are slightly darker in colouration) (Nico et al. 2005). Compared to Silver and Bighead Carp, Grass Carp has fewer, but larger, lateral scales and fewer anal rays (Ross 2001). Grass Carp can also be distinguished from North American cyprinids by the position of the anal fin, which is set far back on the body (Schofield et al. 2005).

To reduce the risk of naturalization following intentional or unintentional introduction, sterile (triploid) Grass Carp have been produced through hybridization (female Grass Carp x male Bighead Carp) or by temperature- and pressure-shocking of eggs (Cassani et al. 2008). Using morphological characteristics, pure diploid Grass Carp can be distinguished from artificially produced hybrids, but this approach is not as successful for distinguishing between pure diploid and pure triploid Grass Carp (Tiwarý et al. 2004). The most important difference between diploid and triploid Grass Carp is the nuclear (and cellular) size of erythrocytes, which is larger in triploid Grass Carp and can be detected using a particle sizer (e.g., Coulter counter) or the more accurate method of flow cytometry (Papoulias et al. 2011). Recently, a new technique to distinguish between diploid and triploid Grass Carp under field conditions has been reported (Krynak et al. 2015). Using a compound microscope, Krynak et al. (2015) found that for triploid Grass Carp, a much larger proportion of erythrocyte nuclei were abnormally shaped (dumbbell or teardrop shaped) than in diploid Grass Carp. Simple examination of blood smears for abnormally shaped nuclei allowed distinction between triploid and diploid Grass Carp. Triploid fish may also have a higher incidence of deformities (Fraser et al. 2012). In a recent study from New York State, sterile triploid Grass Carp from three different locations showed evidence of marked spinal deformity (Grimmett et al. 2011).

DISTRIBUTION

NATIVE DISTRIBUTION

Grass Carp is native to the lakes and ponds and large Asian rivers that generally flow into the Pacific Ocean. Their native range spans from the Amur River basin of southeastern Russia and northeastern China and the Xi ("West") tributary to the Pearl River of southern China, which drains from northeast Vietnam (Adams et al. 2011). Grass Carp occur mainly in the middle and lower reaches of large rivers such as the Yangtze River (Chapman and Wang 2006).

Significant genetic differentiation between the Yangtze, Pearl, and Amur River populations exists, but within the reaches of the Yangtze River there is marginal to no significant difference (Chen et al. 2009a, Liu et al. 2009, Zhao et al. 2011a, Chen et al. 2012a). Genetic diversity of Grass Carp in the Yangtze River has generally been concluded to be low and is attributed to a

small population size and a severe historical bottleneck that occurred during the glacial age (Zhao et al. 2011a). The Yangtze River is the largest river in Asia and harbours the most abundant natural population of Grass Carp (Zhao et al. 2011a) and is considered the evolutionary root of Grass Carp (Chen et al. 2009a, Song et al. 2009).

The future of native Grass Carp populations is of increasing concern as recent studies in the Yangtze and Pearl rivers indicate that Grass Carp abundance is declining (Tan et al. 2010, Duan et al. 2009). See "Conservation Status and Regulation" section for further discussion.

NON-NATIVE DISTRIBUTION

Global

Grass Carp has been introduced worldwide, mainly for the purpose of aquaculture and control of aquatic macrophytes (Table 1). Current records indicate that Grass Carp has been introduced to over 100 countries in various continental regions, including Africa, Asia, Europe, as well as North, South, and Central America (Chen et al. 2009a; Table 1). Of the countries in which Grass Carp has been introduced, it has established in at least 50 and is established in several major Eurasian rivers, including the Amu Darya, Danube, Ganges, Ili, Kuban, Syr Darya, Tone, Ural, and Volga (Chen et al. 2012a, Singh et al. 2013, Bogutskaya et al. 2017). Grass Carp introductions started as early as the 1800s, but most occurred after the 1940s and continue to the present day for aquaculture, improvement of fisheries, sport fishing, control of aquatic weeds, and as food fish (Table 1).

Table 1. Countries Grass Carp (Ctenopharyngodon idella) has been introduced to, current known status, year(s) of first introduction, and purpose for introduction. Status: E = established, PE = probably established, PN = probably not established, N = not established, and ? = unknown. Data are from Froese and Pauly (2015). Occasionally, a country was listed twice with different status reports. In such cases, the less conservative description is reported, as each entry was based on the most reliable references possible.

Country	Status	Year or period of first introduction	Reason for introduction
Afghanistan	PE	1970– 1979	Aquaculture, fisheries
Albania	PN	UN	Aquaculture
Algeria	PN	1985	Fisheries, research
Angola	UN	1980	Aquaculture, fisheries
Argentina	E	1975	Aquaculture, weed control
Armenia	PE	UN	Aquaculture, experimental
Austria	NE	1975	Weed control
Azerbaijan	UN	UN	Aquaculture
Bangladesh	PE	1969	Aquaculture, weed control, fisheries
Belarus	E	1965	Aquaculture, weed control

Country	Status	Year or period of first introduction	Reason for introduction
Belgium	E	1967	Aquaculture, weed control
Bhutan	PE	1983	Aquaculture
Bolivia	NE	1981	Aquaculture
Brazil	PN	1968	Aquaculture, weed control
Brunei	PN	UN	Aquaculture
Bulgaria	PN	UN	Aquaculture
Burundi	NE	1986	Aquaculture
Cambodia	PE	1981	Aquaculture
Canada	NE	1988	Aquaculture, weed control, live food, research
Colombia	NE	UN	Aquaculture
Costa Rica	PE	1976	Aquaculture, weed control
Côte d'Ivoire	E	1979	Aquaculture, weed control
Croatia	UN	UN	Aquaculture
Cuba	E	1966	Aquaculture, weed control
Cyprus	NE	1977	Angling/sport, weed control
Czech Republic*	E	1961	Aquaculture, fisheries (sporting fish)
Denmark	NE	1965	Aquaculture
Dominican Republic	NE	1981	Aquaculture, weed control
Egypt	PE	1969	Aquaculture, weed control
Estonia	NE	1980–1989	Aquaculture, weed control
Ethiopia	E	1975	Aquaculture, weed control
Fiji	PN	1968	Aquaculture, weed control
Finland	E	1970–1979	Aquaculture
France	PE	1957	Aquaculture, weed control
Germany	PE	1964	Aquaculture, weed control
Greece	NE	1980	Fisheries

Country	Status	Year or period of first introduction	Reason for introduction
Guam	UN	UN	UN
Guatemala	PE	1989	Aquaculture, weed control
Guyana	UN	1982	Aquaculture and research
Haiti	UN	1979, 1987, 1990	UN
Hawaii	NE	1968	Aquaculture
Honduras	PE	1976	Aquaculture, weed control
Hong Kong	UN	UN	Aquaculture, weed control
Hungary	E	1963	Aquaculture, sport fishing
India	PE	1959	Aquaculture, weed control
Indonesia	PE	1915	Aquaculture, weed control, research
Iran	E	1966	Aquaculture, weed control
Iraq	E	1985	Aquaculture, weed control
Israel	PN	1965	Aquaculture, weed control
Italy	E	1975-1999	Angling/sport, weed control
Jamaica	UN	UN	Aquaculture, polyculture
Japan	E	1878	Fisheries
Jordan	E	UN	Aquaculture, weed control
Jordan River	E	1965	UN
Kazakhstan	E	1963- 1988	Fisheries
Kenya	PN	1969	Aquaculture, weed control
Korea	UN	1963	Aquaculture
Kyrgyzstan	E	UN	UN
Laos	PN	1977	Aquaculture (food fish)
Latvia	UN	UN	UN
Lesotho	NE	1979	Aquaculture, polyculture
Malawi	NE	1976	Aquaculture

Country	Status	Year or period of first introduction	Reason for introduction
Malaysia	NE	1800– 1899	Aquaculture
Mauritius	PN	1975	Aquaculture, fisheries
Mexico	E	1965	Aquaculture, weed control, fisheries
Moldova	UN	UN	Aquaculture
Mongolia	UN	UN	UN
Morocco	PE	1980–1981	Aquaculture
Mozambique	NE	1991	Aquaculture, fisheries
Myanmar	PE	1967, 1969	Aquaculture
Nepal	NE	1965, 1967	Aquaculture
Netherlands	PE	1966	Angling/sport, weed control
New Zealand	E	1966	Aquaculture, weed control, research
Nigeria	UN	1972	UN
Pakistan	PN	1964	Aquaculture, weed control
Panama	PE	1977	Aquaculture, weed control
Papua New Guinea	UN	UN	UN
Peru	PN	1979	Aquaculture, weed control
Philippines	NE	1964	Aquaculture
Poland	E	1964	Aquaculture, weed control
Puerto Rico	E	1972	Aquaculture, weed control
Reunion	UN	UN	UN
Romania	E	1959	Aquaculture, weed control
Rwanda	PN	1979	Aquaculture, weed control
Saudi Arabia	E	UN	Aquaculture, weed control
Serbia (Yugoslavia)	E	1963	Aquaculture, weed control
Singapore	NE	1900–1999	Aquaculture
Slovakia	PN	1961	Aquaculture

Country	Status	Year or period of first introduction	Reason for introduction
South Africa	PN	1975	Aquaculture, weed control
Sri Lanka	NE	1948	Aquaculture, weed control
Sudan	PE	1975	Aquaculture, weed control
Sweden	NE	1970	Aquaculture, weed control
Switzerland	NE	1974	Aquaculture, weed control
Taiwan	NE	Pre 18th century	Aquaculture, polyculture
Tanzania	NE	1981	Aquaculture, weed control
Thailand	PE	1932	Aquaculture, weed control
Tunisia	PE	1981	Aquaculture, weed control
Turkey	E	1972, 1985	Aquaculture, weed control
Turkmenistan	E	1958– 1961	Aquaculture
Uganda	NE	1979	Aquaculture
UK	PN	1960– 1969	Aquaculture, weed control
Ukraine	UN	UN	UN
United Arab Emirates	UN	1968	Aquaculture, weed control
Uruguay	UN	UN	Research
USA	E	1963	Aquaculture, weed control
USSR (Russian Fed)	E	1949	Aquaculture, fisheries
Uzbekistan	E	1961	Aquaculture
Viet Nam	E	1958	Aquaculture
Zambia	NE	1980– 1989	Aquaculture
Zimbabwe	NE	1995	Aquaculture, weed control

*Dependent on artificial reproduction (Lusk et al. 2010).

North America

Grass Carp was first imported to the United States in 1963 by the United States Fish and Wildlife Service (USFWS), United Nations Food and Agriculture Organization, and Auburn University to evaluate their use as a biological control agent for problematic aquatic vegetation (Mitchell and Kelly 2006). Offspring of these imports, produced at the Fish Farming Experimental Station in Arkansas, are thought to have escaped into the open waters of

Arkansas in 1966 and may very well represent the original unintentional introduction of Grass Carp to the wild (Mitchell and Kelly 2006). By the early 1970s, as the promotion and use of Grass Carp for control of aquatic vegetation increased, records of its occurrence in the wild also began to appear with increasing frequency in rivers in Alabama, Arkansas, Illinois, Florida, Georgia, Mississippi, and Oregon (Mitchell and Kelly 2006, LaVigne et al. 2008). Since its introduction, Grass Carp has continued to spread as a result of research projects, stocking, transport and release, escapes from farm ponds and aquaculture facilities, and natural dispersal from introduction sites (Nico et al. 2014).

To address both the growing concern over the Grass Carp's potential to establish self-sustaining populations in river systems in the United States and the demand for Grass Carp as a biological control for aquatic macrophytes, sterile (triploid) Grass Carp were developed in the late 1970s and the USFWS subsequently implemented the National Triploid Grass Carp Inspection and Certification Program (Conover et al. 2007). The use of triploid Grass Carp has since increased over time, as effective and low-cost solutions are sought by many different agencies to control aquatic macrophyte infestations, some of which are now resistant to chemical control (Conover et al. 2007). Although triploid fish have three sets of chromosomes and are functionally sterile, the induction of triploidy is less than 100% effective. Furthermore, the regulatory environment to control Grass Carp in the United States is fragmented, and both diploid (fertile) and triploid Grass Carp remain available for stocking in private and public waterbodies in the United States (MICRA 2015). Thus the potential remains for Grass Carp to establish in, and spread to, unintended waterbodies remains.

Currently, Grass Carp is the most widely distributed of the Asian carp species in the United States and has been reported in 45 U.S. states (Nico et al. 2014; Figure 2). Established Grass Carp populations have been recorded throughout the Mississippi River drainage basin, including main tributaries such as the Illinois, Missouri, and Ohio rivers, as well as in prairie streams such as the Trinity, Red, and Washita rivers (Hargrave and Gido 2004). However, Grass Carp is not established throughout entire stretches of all rivers or in all tributaries. For example, Grass Carp has not been detected in the upper Missouri River above Gavins Point Dam (South Dakota and Nebraska), or in the Niobara River and Osage River, both tributaries of the Missouri River (Klumb 2007, Wanner and Klumb 2009a, Wanner et al. 2010).

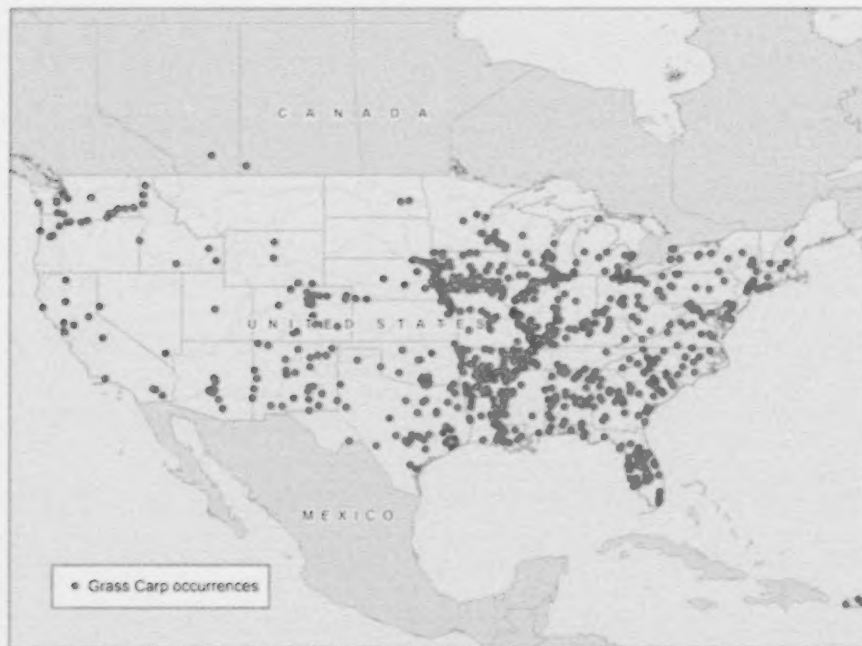


Figure 2. Non-native occurrences of Grass Carp in the U.S. and Canada (1968–2015) as reported in the U.S. Geological Survey (USGS) Nonindigenous Aquatic Species (NAS) database. Map courtesy of the USGS.

In Mississippi, Grass Carp populations appear to be increasing in many rivers within the drainage basin, as evidenced by increasing numbers of Grass Carp in the commercial harvest. In 1996, Grass Carp represented 8% of the total commercial harvest from the Mississippi and Missouri rivers (Nico et al. 2014) but, by 2003, Grass Carp had the fourth highest biomass (1,139 kg, 12%) of commercially caught fish from Missouri River (Iowa) (Conover et al. 2007) and, since 2008, commercial fisherman have harvested 10,889 kg (2008), 29,861 kg (2009), and 14,800 kg (2010) from Iowa and Wisconsin waters of the Mississippi River (WDNR 2011). In the Upper Mississippi River Basin, recent annual harvest data available from state agencies and organizations indicate that harvest levels of Grass Carp have increased (up 78%) in recent years (2000–2005) compared to historic (1989–2005) levels (GLMRIS 2012); however, catch rates for Asian carp, 2010–2013, have been declining on a year-to-year basis, likely indicating that removal efforts are limiting population expansion in the upper Illinois waterway (ACRCC 2014).

There are several artificial or man-made connections through which aquatic invasive species (AIS) can reach the Great Lakes from the Mississippi River basin and vice versa. The Chicago Area Waterway System (CAWS), a permanent man made inter-basin connection between Lake Michigan and the Mississippi River (via the Lower Illinois and Des Plaines rivers), is considered the most important (USACE 2014). The migration of Asian carps through the CAWS is a major concern (ACRCC 2014) and, to prevent their dispersal into the Great Lakes basin through the Chicago Sanitary and Ship Canal (CSSC), a part of the CAWS, electric barriers were deployed (Figure 3). However, since 1990 (>10 years before the electric barriers were constructed), many Grass Carp have been captured within the CSSC and CAWS, on the Great Lakes side of the electric barrier (Kocovsky et al. 2012, USGS 2015). Environmental DNA (eDNA) surveillance

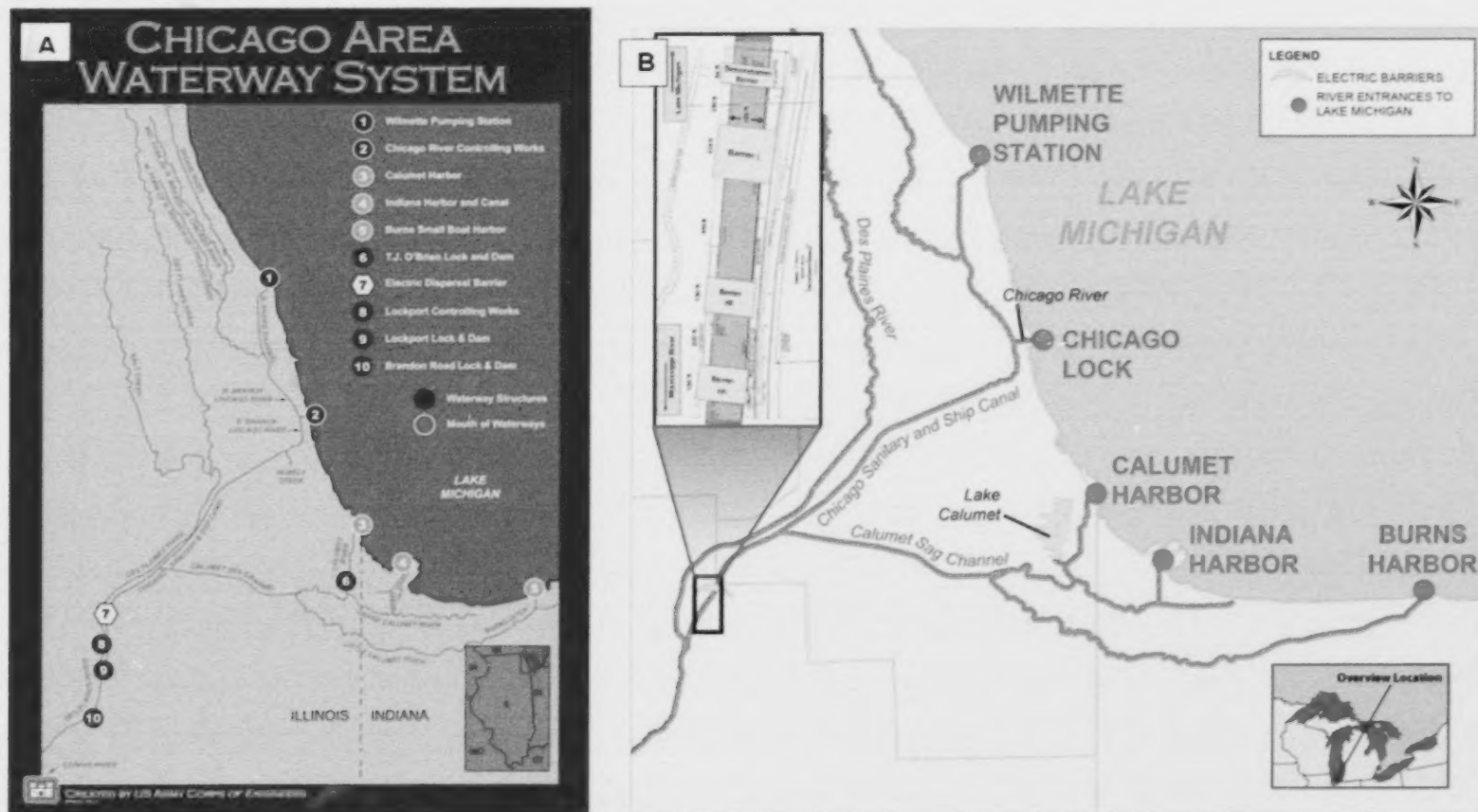


Figure 3. A) Map of the Chicago Area Waterway System (CAWS), B) electric barrier system location (ACRCC 2014).

from the CAWS also indicated the presence of Grass Carp DNA, with 52% of samples (30 of 58) having positive eDNA detection (Wittmann et al. 2014).

Grass Carp captures also continue to be reported from waterbodies in close proximity to the Great Lakes, as well as within all of the Great Lakes, except for Lake Superior (Figure 4). For example, captures have been recorded from Lake Calumet and the Milwaukee, Lower Wisconsin, St. Joseph, Sandusky, Wabash, Kankakee, and Grand (Canada) rivers. Within the Great Lakes basin, both diploid and triploid Grass Carp individuals have been recorded. From 2007–2012, irregular sampling efforts by various agencies revealed the ploidy of 46 feral Grass Carp individuals; diploid individuals were found in Illinois, Minnesota, Michigan, New York, and Ohio, while triploid individuals were found in the states of Illinois, Indiana, Michigan, Ohio, Wisconsin, and New York (Wittmann et al. 2014). However, eDNA surveillance from southern Lake Huron, the western basin of Lake Erie, Lake St. Clair, the Detroit River, the St. Clair River, and the Thames River (Canada) revealed no positive eDNA detections from 2011–2013, which suggests that Grass Carp abundance is sufficiently low as to not be detected using eDNA (Wilson et al. 2014, Wittmann et al. 2014, ACRCC 2014). However, it is noted that the samples tested in Lake Erie were not targeted Grass Carp samples and may, therefore, not be ideally suited to evaluate Grass Carp presence.

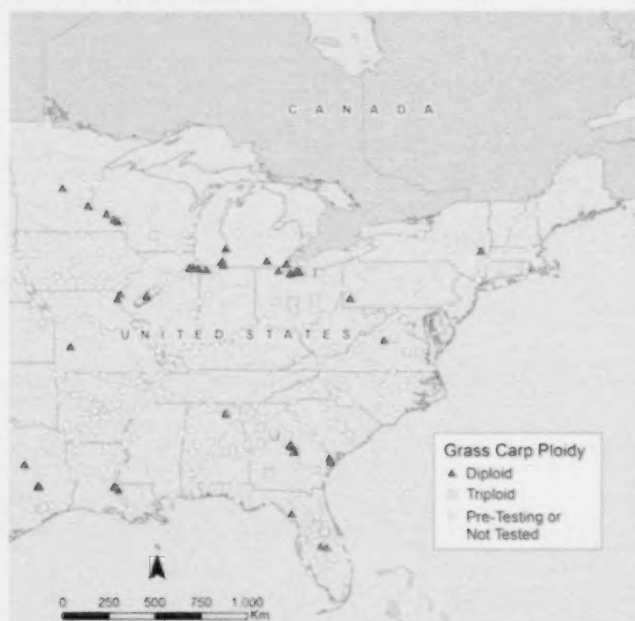


Figure 4. Non-native occurrences of Grass Carp in the U.S. and Canada (1968–2015) as reported in the U.S. Geological Survey (USGS) Nonindigenous Aquatic Species (NAS) database. Ploidy (diploid or triploid) indicated when known (ploidy data courtesy of U.S. Fish and Wildlife Service). Map courtesy of the USGS.

More recently, evidence from otolith microchemistry suggests that four 1-year-old diploid Grass Carp individuals captured from Sandusky River were the result of natural reproduction within the Lake Erie basin (Chapman et al. 2013). Furthermore, Grass Carp collected from the Lake Michigan and Erie basins from 2012–2014 ($n = 35$) were both diploid and triploid specimens, with triploid Grass Carp having an otolith chemistry reflective of aquaculture origin as did diploid fish from Lake Michigan. However, the otolith chemistry for diploids caught in Lake Erie had values reflective of Lake Erie tributaries, providing further evidence that natural recruitment in

the Great Lakes is occurring and is not limited to the Sandusky River (Whitledge 2014). The repeated collection of diploid individuals suggests stock contamination, migration of diploids through connected waterways, and/or the presence of reproductively viable Grass Carp populations in the Great Lakes (Wittmann et al. 2014).

In Canada, single-specimen captures of Grass Carp have occurred since 1985 in all of the Great Lakes except Lake Superior (Cudmore and Mandrak 2004, USGS 2015). Of the approximately eight captures, two were female specimens captured from Lake Huron and were reported to have had developed ovaries (USGS 2015). In 2008, an individual Grass Carp was recorded from Lake Huron, and in the Grand River (a tributary of Lake Erie), an adult Grass Carp was caught in April 2013, and another individual was caught from the same region in August 2013. All three individuals were confirmed to be triploid. Triploid Grass Carp continue to be produced and stocked for aquatic macrophyte control within licensed ponds in the provinces of Saskatchewan and Alberta (Canadian Plains Research Center 2015, Ackenberry Trout Farms 2015).

Finally, a recent study examining microsatellite genetic diversity concluded that Grass Carp established in the Mississippi River basin have lower allelic richness, observed heterozygosity, and within-population genetic diversity than native populations from the Yangtze, Pearl, and Amur rivers (Chen et al. 2012a). Lower genetic diversity in introduced populations may be expected given the small founder population size. However, no genetic bottleneck was detected in the North American population, suggesting that Mississippi River basin Grass Carp has experienced rapid population expansion with potential genetic diversification since its introduction (Chen et al. 2012a). Another study used microsatellite markers to assess population genetic dynamics from three river reaches in the Missouri and Mississippi river basins, found that only slight genetic divergence has occurred since the introduction of Grass Carp to North America and weak evidence to suggest that Grass Carp throughout the basins are reproductively isolated at this time (Adams et al. 2011). The most likely origins of colonized populations in the Mississippi River are the Yangtze, Amur, and Pearl rivers (Song et al. 2009).

Predicted North American Range

A number of recent studies have employed different modelling and mapping techniques to predict where Grass Carp could establish in North America. These studies made predictions at different scales, ranging from the size of a river to the entire continent. In a smaller-scale study in the Pacific Northwest, the environmental conditions of the lower Columbia River (downstream of confluence with the Snake River) were evaluated for the potential for Asian carps to arrive, survive, and reproduce in the basin (Aitkin et al. 2008). Variables were concluded to be conducive to adult survival, as stocked triploid Grass Carp survive in small lakes and ponds throughout Washington, Oregon, and Idaho, and Grass Carp have been observed in both the Columbia and Snake rivers. Dams were considered unlikely to impede movement, as migrating Grass Carp have been found using fish ladders within the river (Aitkin et al. 2008). Findings from the cursory evaluation of environmental conditions indicated that habitat characteristics, water temperatures, discharge and velocity appear conducive for adult survival, spawning, and egg and larval survival of Asian carps; however, water hardness (below 100 mg/l CaCO_3 in the Columbia and Snake rivers) may hinder embryonic development. To better assess the risk of introduction, the authors noted the need for further research within introduced ranges and for the relationship between water hardness and egg and larval survival to be further evaluated as results vary across studies.

Six studies opted for a broad-scale approach and made predictions with respect to potential establishment throughout North America. The first study focused on the mean annual air temperature range in the native range to predict the potential distribution of Grass Carp in North

America (Mandrak and Cudmore 2004). The distribution of suitable thermal habitat was widespread in the U.S. and Canada; thus, if Grass Carp successfully colonizes the Great Lakes basin, there is a high probability that its potential distribution would extend north to 60°N. The authors noted that the potential distribution of Grass Carp can be further refined based on the distribution and availability of spawning and feeding habitats. Within the Canadian portion of the Great Lakes, there is a large amount of vegetated shoreline that could provide suitable food and there are many tributaries to the Great Lakes that may be suitable spawning rivers (Mandrak et al. in prep.). In a study on the thermal and hydrologic suitability of Lake Erie, three tributaries to western and central Lake Erie (Maumee, Sandusky, and Grand rivers) were predicted to be the most likely to support spawning of Asian carps (Kocovsky et al. 2012).

The other five studies employed ecological niche-based modelling using a combination of environmental parameters to predict potential North American range expansion. Chen (2008) used Genetic Algorithm Rule-set Prediction (GARP) that incorporated topographic and climatic conditions (15 environmental variables) from both Asia and North America and a total of 93 unique occurrence points from their native distribution. The predicted range encompassed 49 of 54 established points available for testing from the coterminous U.S. and included the states of Arkansas, Kentucky, Illinois, Louisiana, Missouri, Mississippi, Tennessee, and Texas (Figure 5). The niche models also predicted that areas in Washington, Oregon, northern California and northern Idaho, southeastern Canada, and the Great Lakes drainages are suitable for Grass Carp. Chen (2008) did not assess the Great Lakes themselves.

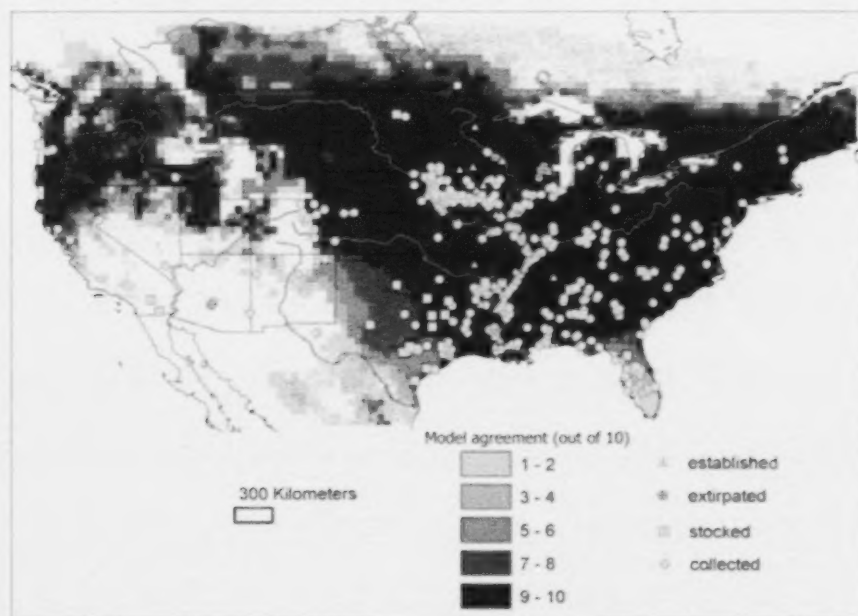


Figure 5. Predicted distribution of Grass Carp (*Ctenopharyngodon idella*) in North America. The map shows the 10 best distributions according to Genetic Algorithm for Rule-set Prediction (GARP). GARP used niche-based modelling based on such variables as topography and climate, and extrapolated the potential non-native range based on ability to predict the native range. Dark red indicates 9–10 of the 10 best models predicting presence, firebrick 7–8, red 5–6, salmon 3–4, and pink 1–2. Figure and caption modified from Chen (2008).

DeVaney et al. (2009) also employed GARP to generate niche models from topographic and climatic variables (15 environmental data layers) that summarize aspects of the ecological landscape from both the native and introduced ranges. The best Grass Carp models were

projected onto central North America (~25–54°N) and predicted a broad geographic range across the eastern, central, and northwestern United States, including some parts of southern Canada (Figure 6). The potential range encompassed 36 of 47 occurrence points available for testing from North America and included establishment in the Great Lakes drainage, but did not extend as far north as the niche models from Chen (2008) and Herborg et al. (2007).

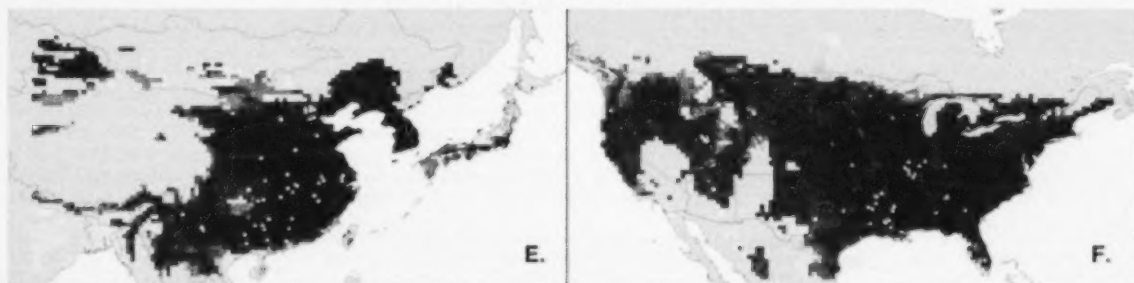


Figure 6. Potential distribution of Grass Carp (*Ctenopharyngodon idella*) in North America. Map is based on environmental data layers for native and introduced ranges. Shading indicates the predicted suitability (brick red=7–10 models, canary red =4–6 models, pink=1–3 models. Occurrence points represent independent validation data in the native or introduced ranges (DeVaney et al. 2009).

Herborg et al. (2007) used ecological niche-based GARP models to predict suitable environments in North America for where Grass Carp can survive. The Grass Carp model was developed based on its reported native range and the associated global climatic and geographic coverages. Mean daily precipitation was the most important predictor of species presence and contributed 39.8% to prediction accuracy in the Grass Carp model, while the minimum and mean daily air temperature contributed 24.4% and 14.2% to prediction accuracy, respectively. The most suitable habitat was in areas with a mean daily precipitation of >5–15 mm and <50–60 mm and a minimum temperature of -11 to 4 °C. The importance of precipitation was probably related to high spring flow requirements in large rivers. Only two established populations of Grass Carp were recorded in areas with an environmental suitability of <85%. The authors noted that inclusion of flow data, water temperature, and water chemistry, if they had been available, could have improved the models. Based on the niche model, Grass Carp could expand across most of Canada, excluding the far north (Figure 7). This is in contrast to the model developed by DeVaney et al. (2009), which did not extend as far north; disparity could have resulted from the use of different criteria for selecting points in the native range. For example, the use of points based on museum records underestimates the extent of native range habitat, whereas the use of random points derived from range maps could result in an overestimation of range (Herborg et al. 2007). Different model outcomes could have also been attributed to differences in the way environmental variables were selected.

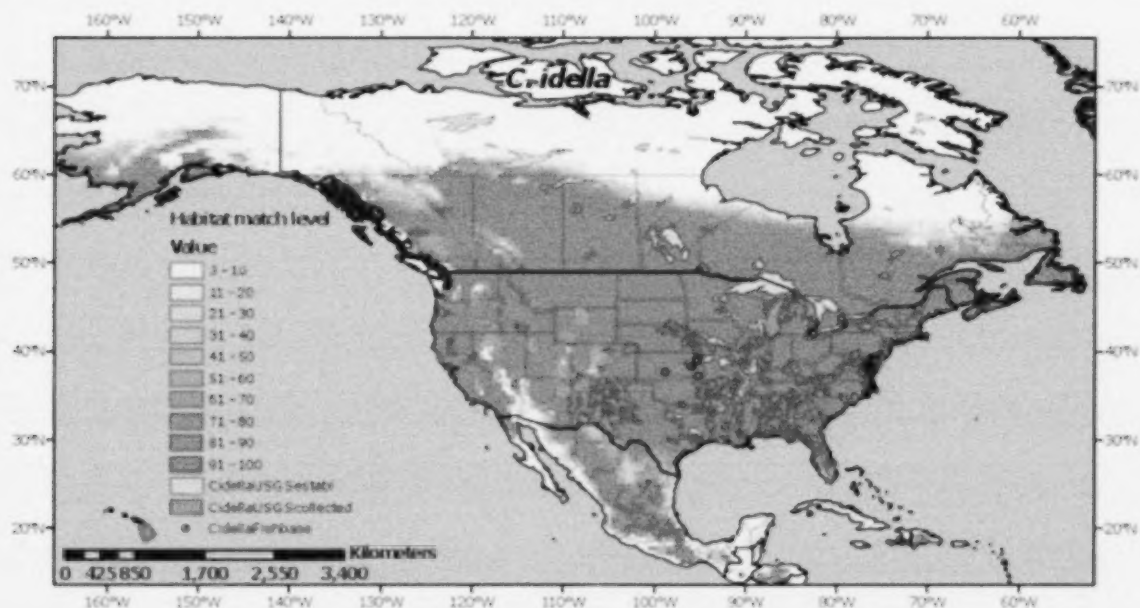


Figure 7. Potential distribution of Grass Carp (*Ctenopharyngodon idella*) in North America. Maps are based on environmental suitability, or the number out of a maximum of 100 niche-based models that predicted a certain area as appropriate. Figure and caption modified from Herborg et al. (2007).

A recent study estimated the potential geographic extent of Grass Carp within the Great Lakes region (and North America) with seven machine-learning methods of classification that used environmental information (air temperature variables and growing degree days) and information-rich species occurrence data primarily from outside North America to train models of potential species distribution (Wittmann et al. 2014). Species distribution models predicted that Grass Carp is likely to encounter conditions suitable for establishment throughout much of the eastern U.S. and Canada, and that suitable Grass Carp habitat occurs in all five Great Lakes, but predicted a low probability of survival of Grass Carp in Lake Superior and northern portions of lakes Huron and Michigan (Figure 8). For example, nearshore areas with macrophyte growth were often classified as environmentally suitable in all but Lake Superior. The species distribution models used in this study have reduced uncertainty associated with model training data compared to the studies previously described; however, models from this study still do not address species-specific habitat requirements in determining the likelihood of establishment.

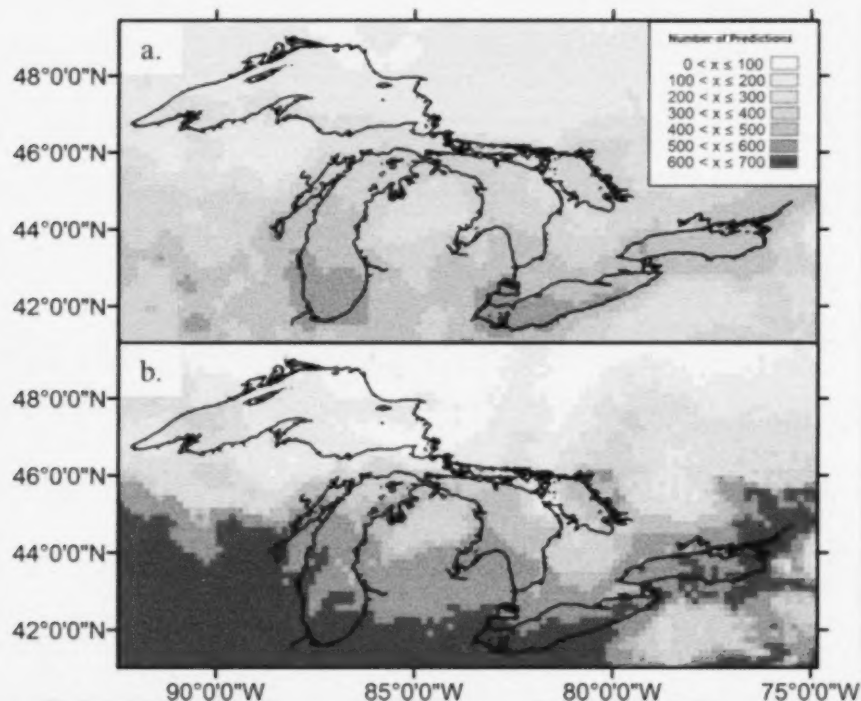


Figure 8. Predicted potential distribution of Grass Carp (*Ctenopharyngodon idella*) in the Great Lakes region based upon (a) native range occurrence data with bootstrapping to represent uncertainty and (b) native range data supplemented with randomly selected 'established' occurrence information for training. Figure and caption modified from Wittmann et al. (2014).

The authors note that incorporation of location-specific habitat layers into species distribution models would refine assessments of the likelihood of establishment. The most recent species distribution modelling (SDM) efforts do, however, involve using species distribution models with predicted distribution, and then restricted by habitat data layers (submerged aquatic vegetation and wetland) for the Great Lakes specific to the physiological limitations of Grass Carp (Wittmann et al. 2016a). The resulting predicted Grass Carp distribution was then assessed further by incorporating the predicted suitable *Hydrilla verticillata* habitat in the Great Lakes region, which expanded its forecasted distribution relative to SDM outputs restricted only by the current macrophyte distribution (Figure 9). Integrated risk maps generated by this approach may help provide a more scientifically informed prediction of species distribution.

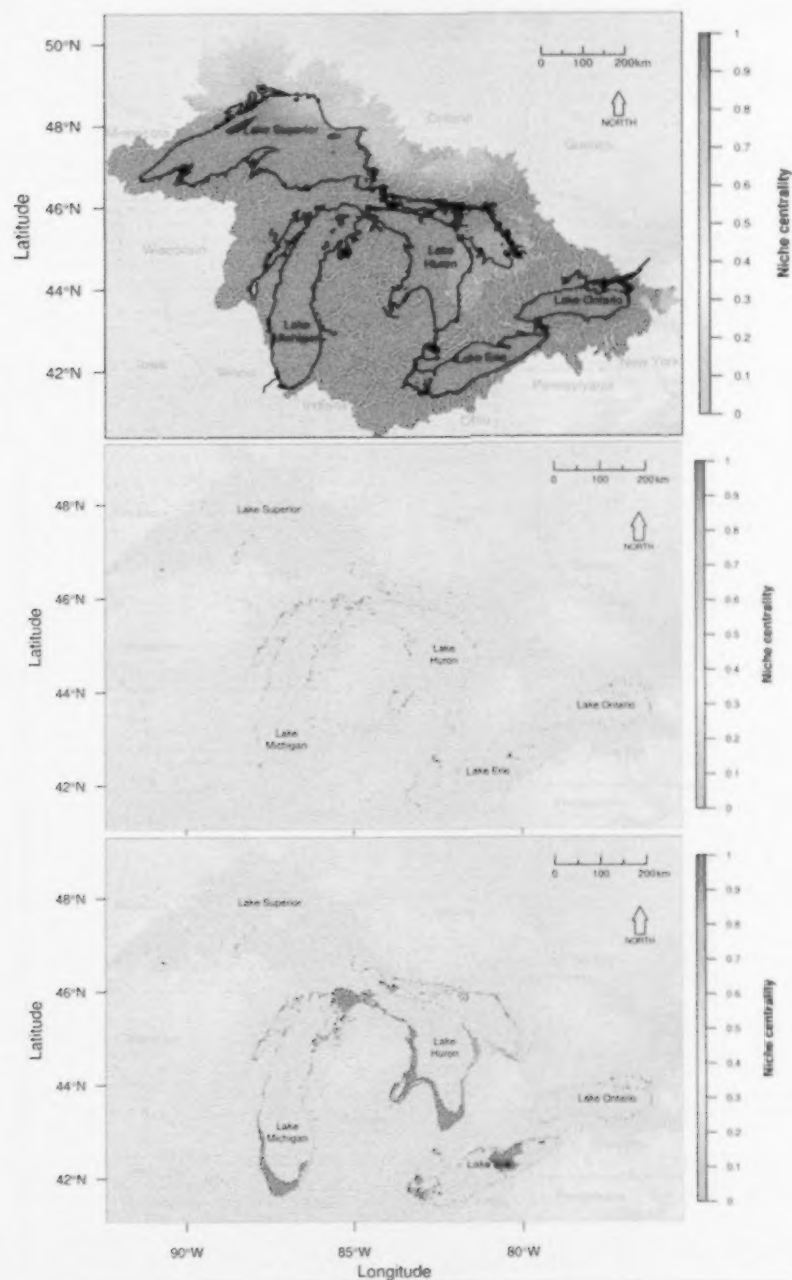


Figure 9. Predicted potential distribution of Grass Carp (*Ctenopharyngodon idella*) in the comprehensive Great Lakes watershed region. Using niche centrality (top panel), clipped using a submersed aquatic vegetation and wetlands layer (middle panel), and a combined SAV, wetlands and predicted *Hydrilla verticillata* niche (c; bottom panel). High values of niche centrality indicate climate conditions in the Great Lakes basin fall generally within the predicted niche. Figure and caption modified from Wittmann et al. (2016a).

BIOLOGY AND NATURAL HISTORY

A large amount of literature on the biology of Grass Carp exists; however, much of it is focused on carp production for aquaculture as opposed to wild populations. This synopsis focuses on the biology of Grass Carp in the wild, although studies from aquaculture practices are included if relevant aspects of life history are investigated.

AGE AND GROWTH

Growth in Grass Carp is a function of many factors, including age, size, habitat, and season (Cudmore and Mandrak 2004). In addition, size and age data can vary depending on sampling size, sampling gear, season, and habitat (Wanner and Klumb 2009a) and should, therefore, be interpreted with caution. Age determination techniques also need to be validated. Various aging techniques to assess population dynamics of Bighead and Silver carps have been used and may be applied to estimate fish age analysis for Grass Carp (Chapman et al. 2013). Otolith annuli have been used to identify differences in growth patterns between hatchery-reared and wild juvenile Grass Carp (Song et al. 2003), and daily growth of lapilli and the formation of the first increment one day after hatching have been verified for Grass Carp (Zhang et al. 2012).

Using scales, postcleithra, ossified fin rays, and vertebral sections, Chapman et al. (2013) estimated the age of four Grass Carp (Total Length [TL] size range at capture: 450–550 mm) from the Sandusky River, Ohio to be age 1+. The back-calculated length at age resulted in estimated lengths at the first annulus of 158–186 mm, which is small for Grass Carp at that age at similar latitude but consistent with the temperature and hydrograph conditions in 2011 and 2012 when fish were estimated to have spawned (Chapman et al. 2013). Three other individuals caught had a similar range in length at age 1 (196–248.7 mm), as determined by back-calculation using scales and vertebral sections (D. Chapman, U.S. Geological Survey (USGS), pers. comm.). Length at age was back-calculated for a further seven Grass Carp captured in the Great Lakes basin between 2013 and 2014 (P. Kocovsky, USGS, pers. comm.). Fish ranged in age from 9 to 18 years old and were between 781 and 1228 mm at capture. Average lengths at age were back-calculated: 255 mm (age 1), 463 mm (age 2), 571 mm (age 3), 650 mm (age 4), 710 mm (age 5), 764 mm (age 6), 801 mm (age 7), 830 mm (age 8), 860 mm (age 9), 887 mm (age 10), 911 mm (age 11), 936 mm (age 12), 955 mm (age 13), 897 mm (age 14), 950 mm (age 15), 1005 mm (age 16), 1042 mm (age 17), 1069 mm (age 18). In a report for Illinois Department of Natural Resources (Whitledge 2014), Grass Carp specimens (diploid and triploid) collected 2013–2014 from the Great Lakes basin were also assessed for size at age: 597 mm (age 3), 985 mm (age 6), 955 mm (age 7), 954 mm (age 8), 1092 mm (age 9), 1079 mm (age 10), and 935 mm (age 12).

Otolith growth patterns of two wild-caught Grass Carp (likely escaped aquaculture fishes) in New Zealand revealed a slower growth rate for a lake-caught fish (6+-year-old, 1.65 kg, 435 mm fork length; FL) compared to an individual captured from a canal (3+-year-old, 3.1 kg, 570 mm FL) (Baker and Smith 2006). Growth of the lake-caught Grass Carp was similar to that of a 5-year-old hatchery-reared Grass Carp (1.14 kg, 437 mm Fork Length [FL]).

Studies from American rivers have recorded size (length and weight) data of Grass Carp. Between 2003 and 2007, adult Grass Carp condition was investigated in the Missouri River, from Gavins Point Dam to its confluence with the Mississippi River (Wanner and Klumb 2009a, b). Grass Carp lengths and weights ranged 307–1080 mm and 0.33–12.97 kg ($n = 624$), respectively; and, condition of established populations from two reaches of the Missouri River did not differ (Wanner and Klumb 2009b). However, the authors noted that Asian carps are wary to capture, which limits the ability to accurately describe their condition and estimates of average and maximum sizes will likely vary depending on fishing gear. Similar length-weight

values were found in 2008–2009 by a study assessing Grass Carp population structure using fish collected from Missouri River by electrofishing (Adams et al. 2011). Grass Carp caught ranged from 101–973 mm with corresponding weights ranging 0.01–10.37 kg (n=56). In 1999 and 2000, juvenile Grass Carp from Lake Texoma (Texas and Oklahoma) averaged 24.7 mm TL and ranged in length from 15.2–60 mm with two apparent size modes of 18 mm TL and 41 mm TL (Hargrave and Gido 2004). Grass Carp caught in the Great Lakes basin 2011–2014 showed a length-weight relationship described as $W=0.0122(L)^{3.0116}$ ($R^2=0.9704$, Figure 10) (data obtained from USGS 2015, Whittedge 2014).

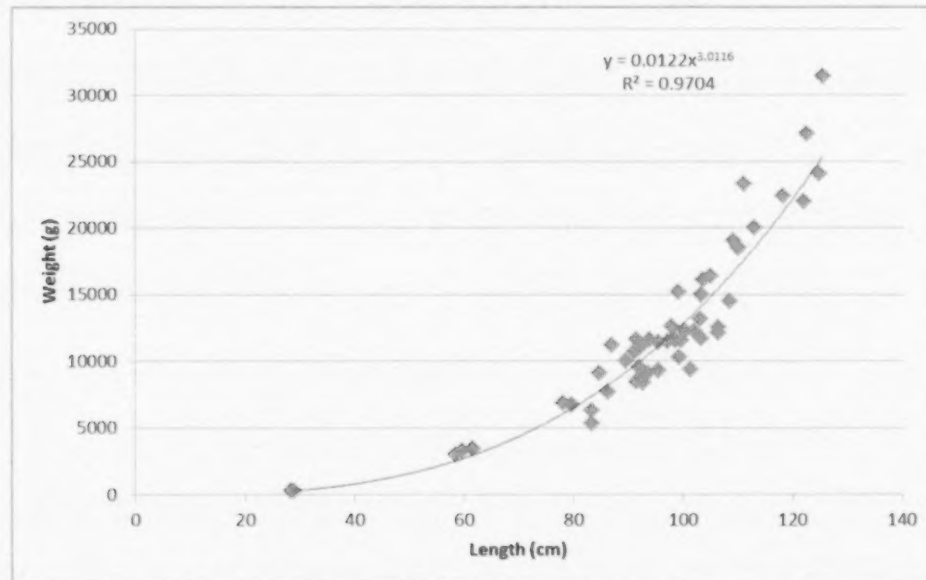


Figure 10. Length-weight relationship for Grass Carp caught in the Great Lakes basin from 2011–2014. Data from USGS database (2015).

Triploids are expected to have a higher growth potential due to sterility and reduced gonadal development but growth performance between diploids and triploids vary between species (Tiway et al. 2004) and remains unclear for Grass Carp. In the Santee Cooper reservoir systems of South Carolina, triploid Grass Carp were stocked from 1989 to 1996 (Kirk and Socha 2003). Subsequent collections through 1998 to 2002 revealed that body condition ranged from 0.83 to 1.0, a maximum age of 11 years, and total annual mortality rates of 22–39%, meaning that 10% of a cohort could persist for 5–9 years. Triploid Grass Carp were also stocked in Lake Gaston, Virginia-North Carolina beginning in 1995 to control Hydrilla (*Hydrilla verticillata*). Between 2006 and 2010, bowfishers collected 243 Grass Carp aged 1–16 years old from the lake (Stich et al. 2013). Length-weight relationships were generated to predict the weight of Grass Carp at each age from back-calculated lengths at age. The relationship between total length (TL, mm) and weight (W, g) was $W = (3.25 \times 10^{-5}) \times TL^{2.87}$ suggesting that Grass Carp become less rotund as their length increases. The relationship between weight (g) and age (years) was nearly linear, but growth was highly variable within age classes. The von Bertalanffy growth model predicted TL at each age by the equation: $L_t = 1297[1 - e^{-0.135(t+1.52)}]$ where L_t is length at age t .

In the native range, Grass Carp larvae were sampled in 2007 from three locations within the Yangtze River. Larvae ranged from 5.1 to 8.0 mm (notochord length) and were 6–11 days of age, whereas, juveniles ranged from 30.0 to 206.6 mm (standard length) and were 20–76 days

of age (Zhang et al. 2012). Width of the first increment was usually 5 μm and the maximum daily increment width was 10 μm at 21 days of age. Decreased larval growth in juveniles from Dongting Lake was attributed to the site's proximity to the Three Gorges Dam. The length-weight relationship for Grass Carp from the Great Lakes basin is similar to that derived from numerous studies for the native range: $W = 0.0229(L)^{2.92}$ ($n = 8$; Froese and Pauly 2015), and $W = 0.0350(L)^{2.781}$ (Zhao and Wang, OMNRF, unpubl. report).

Based on an extensive literature review for growth of Grass Carp, Wittmann et al. (2016b) compiled a global growth rate (g day^{-1}) dataset for those studies for which either stocked or wild populations of Grass Carp were not artificially fed (e.g., with pellets or other supplements) and which had a minimum experimental period of 6 months or greater (Table 2). Wittmann et al. (2016b) calculated growth rate values for those studies that did not report growth as g day^{-1} and included information on fish age and presence of macrophytes when available. While growth rate of stocked Grass Carp did not show a relationship with SDM (Maxent) estimates of habitat suitability, growth rate of wild Grass Carp populations increased with predicted habitat suitability (Wittmann et al. 2016b).

To optimize aquaculture production, numerous studies have investigated the effect of stocking density, species composition, and proportion of species on the daily weight gain (DWG) and specific growth rate (SGR) of Grass Carp. Two polyculture experiments in Brazil revealed differences in the mean DWG or SGR of Grass Carp fingerlings (0.9–3.27 g initial weight) across varying proportions, densities, and species compositions. Mean DWG of fingerlings in the two studies was 0.5–2.65 g day^{-1} and mean SGR was 1.34–2.27 $\% \text{ day}^{-1}$, with the highest gain occurring in treatments incorporating species other than carp as well as in treatments with an increased number of species (Bolognesi da Silva et al. 2006, Barcellos et al. 2012). In Saudi Arabia, average daily growth rates of stocked Grass Carp fingerlings (average initial weight of 3.3 ± 0.3 g) was 2.60–4.11 g day^{-1} , and increased with stocking density (Belal 2007). Another study, carried out in South India, investigated the growth performance of carps under extensive composite culture (stocked at 1500 fish/ha) in a hardwater (mean = 510.5 ± 258.5 ppm) seasonal pond (Athithan and Sanjeeviraj 2009). Over 300 days, stocked Grass Carp grew from an average initial weight and length of 0.9 g and 3.2 cm, to 550 g and 22 cm, respectively, representing an estimated average DWG of 1.83 g day^{-1} . In Uzbekistan, Grass Carp ($n = 150$) growth and maturation under pond conditions (average lowest daily temperature = -1 $^{\circ}\text{C}$; average highest daily temperature = 27 $^{\circ}\text{C}$) was investigated over 3 years (Kamilov and Komrakova 2003). Grass Carp at age 1 had a mean length of 22.3 cm, age 2 (37.2 cm), age 3 (52.7 cm), and age 4 (68.6 cm), with the relationship between weight and length described by $W = 0.027 \times L^{2.89}$.

Extensive research has also been carried out on Grass Carp growth to identify the most cost-effective diet and feeding rate for producing Grass Carp for human consumption and biotic control. Such studies, while not directly relevant to natural conditions, can provide estimates of growth rates under optimal aquaculture conditions, which can be considered to be maximal values. In China, the SGR of juvenile Grass Carp (initial weight 6.52 g) fed diets with different lipid levels ranged from 0.85 to 1.30 and a maximal weight gain of 148.5% was reported during the 70-day experiment (Du et al. 2005). In a feeding rate experiment, SGR of stocked juvenile Grass Carp (initial weight 3.08 ± 0.03 g) ranged from 0.67 to 1.15 (Du et al. 2006), while another study investigating the effect of dissolved oxygen and dietary lysine (initial weight 4.11 ± 0.03 g) reported SGR values ranging from 2.74 to 3.79, and a maximal weight gain of 775% with lowest values occurring in the low dissolved oxygen and low lysine treatments (Gan et al. 2013). In a series of experiments investigating optimal dietary levels of various elements (phosphorus, potassium, magnesium, zinc, lysine, and calcium), hatchery-reared juvenile Grass Carp (3.15–7.69 g initial weight) had weight gains of 166–366% and SGRs of 1.11–2.75% day^{-1} (Wang et

Table 2. Global Grass Carp growth rates; included only studies where the minimum period was 6 months or greater (Wittmann et al. 2016b). Wittmann et al. (2016b) provides the full references for these data.

ID	Location	Lat	Long	Stocking rate (fish/ha)	Experimental Period (years)	Fish Age (years)	Avg Growth (g/day)	Wild (w) / Stocked (s)	Macrophytes present
8	Lake Wales, FL, USA	27.90	-81.58	?	4.0	4	10.2	s	<i>Hydrilla verticillata</i>
9	Lake Baldwin, FL, USA	28.57	-81.32	24	2.0	4	11.5	s	<i>Hydrilla verticillata</i>
12	Malacca, Malaysia	2.21	102.26	147	1.1	?	8.3	s	<i>Pennisetum purpureum</i>
13	India (Cuttack)	20.46	85.88	321	1.6	2	4.7	s	<i>Hydrilla verticillata</i> , <i>Lagarosiphon</i>
14	India (Kalyani)	22.99	88.45	500	1.0	Fingerling	13.6	s	<i>Hydrilla verticillata</i>
15	India (Uttar Pradesh)	27.64	80.08	500	0.5	Fingerling	9.9	s	<i>Hydrilla verticillata</i>
16	India (Haryana)	29.07	76.09	500	1.0	Fingerling	5.7	s	<i>Hydrilla verticillata</i>
18	Lake Guntersville, AL, USA	34.37	-86.32	Unknown	NA	5	3.8	w	<i>Hydrilla verticillata</i> , <i>Myriophyllum spicatum</i>
21	Hong Kong	22.44	114.12	875	2.0	2	1.7	s	Common grass, aquatic plants, silkworm faeces, mulberry leaves
24	Malacca, Malaysia	2.24	102.26	1013	0.7	Yearling	5.8	s	<i>Hydrilla verticillata</i>
27	Turkmenia	38.99	59.02	?	1.5	2	3.2	s	Various
28	Rumania	45.78	24.88	?	1.5	2	1.8	s	Various
29	Hungary	47.49	19.05	?	1.5	2	3.6	s	Various
30	Sudan	16.30	30.70	91 fish introduced	3.5	?	3.5	s	<i>Potamogeton</i> spp., <i>Lemna</i> spp., <i>Elodea</i>
31	Siberia	61.01	99.21	?	?	?	2.8	s	Unknown
32	Turkmenia	38.99	59.02	?	?	Yearling	3.3	s	Unknown

ID	Location	Lat	Long	Stocking rate (fish/ha)	Experimental Period (years)	Fish Age (years)	Avg Growth (g/day)	Wild (w) / Stocked (s)	Macrophytes present
33	Israel	31.00	34.87	?	?	Yearling	8.2	s	Unknown
34	Malacca, Malaysia	2.21	102.26	12 fish studied, no indication of pond/system size	4.3	Yearling	9.2	s	Unknown
36	South Africa	-29.81	31.00	150-200	2.5	Fingerling	6.7	s	<i>Vallisneria spiralis</i>
38	Sandusky River, OH, USA	41.43	83.06	NA	NA	1	4.1	w	Unknown
39	Lake Gaston, Virginia/North Carolina, USA	36.50	-77.93	?	5.0	9	3.6	s	<i>Hydrilla verticillata</i>
40	South Dakota, USA	42.85	-97.52	480	0.4	Yearling	3.5	s	<i>Najas guadalupensis</i> , <i>Chara sp.</i> , and <i>Potamogeton pectinatus</i>
41	Haryana, India	29.43	76.58	37	1.2	?	18.8	s	<i>Hydrilla verticillata</i>
41	Haryana, India	29.43	76.58	37	0.8	?	21.3	s	<i>Hydrilla verticillata</i>
42	Germiston Lake, South Africa	-26.23	28.16	3	2.0	<1	7.7	s	<i>Potamogeton pectinatus</i>
43	São Jerônimo, Rio Grande, Brazil	-29.95	-51.72	150	0.5	?	0.7	s	<i>Luziola peruviana</i>
44	Augusta, GA, USA	33.42	-82.14	80	1.0	1+	3.5	s	<i>Eleocharis</i>
45	Waikato, New Zealand	-38.06	175.44	83	0.7	?	10.6	s	<i>Ceratophyllum demersum</i> , <i>Myriophyllum aquaticum</i> , <i>Potamogeton spp.</i> , <i>Polygonum spp.</i>
46	Suwanee Lake, Florida, USA	28.36	-82.23	299	1.8	?	3.2	s	<i>Hydrilla verticillata</i> , <i>Najas spp.</i>

ID	Location	Lat	Long	Stocking rate (fish/ha)	Experimental Period (years)	Fish Age (years)	Avg Growth (g/day)	Wild (w) / Stocked (s)	Macrophytes present
47	Broward Lake, Florida, USA	29.51	-81.59	118	1.8	?	6.4	s	<i>Hydrilla verticillata</i> , <i>Najas</i> spp.
48	Onnaike and Maie Pond, Japan	36.65	138.18	98	1.0	<1	3.2	s	<i>Myriophyllum spicatum</i> , <i>Ceratophyllum demersum</i> , <i>Potamogeton</i> spp., <i>Hydrilla verticillata</i> , <i>Trapa</i> spp.
49	Yaits Arm, Ural River Delta, Russia	46.88	51.66	1513 fish placed in these rivers	8.0	2	3.6	w	<i>Spirogyra</i> spp. known to grow in this area
50	85 km from Astrakan, Russia	46.89	47.59	1513 fish placed in these rivers	9.0	2	4.5	w	<i>Spirogyra</i> spp. known to grow in this area
51	Red Haw Lake, Iowa, US	41.00	-93.27	27	3.2	?	5.5	s	<i>Potamogeton</i> , <i>Najas</i> , <i>Ceratophyllum</i> , and <i>Elodea</i>
52a	Waihi Beach Reservoir, New Zealand	-37.40	175.88	50-100	2.0	4 - 6 years old	5.6	s	<i>Potamogeton ochreatus</i> , <i>Eleocharis sphacelata</i> , <i>Spirogyra</i> spp., <i>Zygnema</i> spp., <i>Mougiotia</i> spp., <i>Typha orientalis</i> , <i>Egeria densa</i> , <i>Nitella hookeri</i>
52b	Parkinson's Lake, New Zealand	-37.31	174.68	6 to 44	1.0	5 - 6 years old	7.3	s	<i>Potamogeton ochreatus</i> , <i>Eleocharis sphacelata</i> , <i>Spirogyra</i> spp., <i>Zygnema</i> spp., <i>Mougiotia</i> spp., <i>Typha orientalis</i> , <i>Egeria densa</i> , <i>Nitella hookeri</i>
53	Auburn, AL, USA	32.58	-85.50	74	0.7	1 to 2	11.0	s	Unknown

ID	Location	Lat	Long	Stocking rate (fish/ha)	Experimental Period (years)	Fish Age (years)	Avg Growth (g/day)	Wild (w) / Stocked (s)	Macrophytes present
55	Lake Conroe, Texas	30.43	-95.60	18	0.8	1-4 years	7.5	s	<i>Hydrilla verticillata</i> , <i>Ceratophyllum demersum</i> , <i>Myriophyllum spicatum</i> and 14 other species
56	Al-Hassa, Saudi Arabia	22.28	50.68	30000	2.0	Fingerlings + 4 weeks	3.2	s	<i>Phragmites</i> , <i>Ceratophyllum</i> and <i>Cladophora</i>
57a	Shinfield Lake, South Midlands, England	51.41	-0.94	221	1.7	301 g	0.3	s	<i>Myriophyllum spicatum</i> , <i>Potamogeton natans</i> , <i>Nymphaea alba</i> , <i>Ceratophyllum</i>
57b	Nether Whorton Lake, South Midlands, England	51.98	-1.32	325	5.6	200 g	0.4	s	<i>Potamogeton crispus</i> , <i>Ranunculus pelatus</i> , <i>Sparganium erectum</i>
57c	Pusey Lake, South Midlands, England	51.66	-1.59	717	3.5	Size range from 40 g to 500 g	0.8	s	<i>Callitriche stagnalis</i> , <i>Potamogeton pectinatus</i> , <i>Vaucheria sessilis</i> , <i>Spirogyra</i> spp., <i>Tribonema</i> spp.
58	Gezira, Sudan	14.88	33.44	91 fish stocked, area not indicated	3.5	Fingerling + 2 months	3.5	s	<i>Potamogeton</i> , <i>Chara</i> , <i>Najas</i> spp.
59	Dgal Wielki, Jezioro, Poland	54.11	21.79	15	1.0		1.9	s	<i>Potamogeton</i> spp., <i>Lemna</i> spp., <i>Elodea</i>
60	Vodňany, Czech Republic	49.15	14.18	126	1.0	?	1.4	s	<i>Cladophora glomerata</i> , <i>Potamogeton pectinatus</i> , <i>Myriophyllum</i> , <i>Sparganium</i> and <i>Elatine</i>
61	Suwannee Pond, FL, USA	30.30	-82.98	299	2.8	?	2.1	s	<i>Hydrilla verticillata</i>
61	Madison County, FL, USA	30.46	-83.51	52	2.8	?	4.0	s	<i>Hydrilla verticillata</i>

ID	Location	Lat	Long	Stocking rate (fish/ha)	Experimental Period (years)	Fish Age (years)	Avg Growth (g/day)	Wild (w) / Stocked (s)	Macrophytes present
61	Pasco Pond, FL, USA	28.22	-82.45	228	2.8	?	0.4	s	<i>Hydrilla verticillata</i>
61	Broward Lake, FL, USA	29.51	-81.59	118	2.8	?	4.4	s	<i>Hydrilla verticillata</i>
62	Davis, CA, USA	38.55	-121.74	45	1.2	?	2.0	s	<i>Myriophyllum spicatum</i> , <i>Chara</i> sp. <i>Potamogeton pectinatus</i> ,
63	Marion, AL, USA	32.63	-87.32	123	0.5	Fingerling	7.4	s	<i>Pithophora</i> sp., <i>Najas</i> sp.
64	Bay of Plenty, New Zealand	-37.70	176.16	64	0.6	2	0.8	s	<i>Callitriche stagnalis</i> , <i>Nasturtium officinale</i>
65	Ueda City, Japan	36.40	138.25	30-100	2.0	2	4.3	s	<i>Ceratophyllum demersum</i> , <i>Myriophyllum spicatum</i> , <i>Hydrilla verticillata</i> , <i>Potamogeton crispus</i> , <i>Trapa natans</i> , <i>Phragmites communis</i> , <i>Zizania latifolia</i> , <i>Scirpus fluvialis</i> , <i>Glyceria acutiflora</i>
66	Netherlands	51.97	5.67	285	0.5	?	1.8	s	<i>Chara</i> , <i>Glyceria fluitans</i> , <i>Alisma plantago aquatica</i> , <i>Callitriche</i> sp., <i>Polygonum amphibium</i> , <i>Typha</i> sp.,
68	Amur River at Leninskoe, Russia	47.93	132.63	NA	1.0	?	1.9	w	Unknown
69	Lake Bolon and canals, Russia	49.83	136.37	NA	1.0	?	0.3	w	Unknown
70	Lake Udy'l, Russia	52.13	139.85	NA	1.0	?	1.0	w	Unknown

al. 2005, Wang et al. 2011, Liang et al. 2012 a, b, c, d, Liang et al. 2014). Under optimum dietary chromium picolinate levels, Grass Carp fingerlings with initial weight of 12.42 g had a weight gain of 479.64% (Liu et al. 2010). In India, female yearlings (average initial length 44.1 ± 0.3 cm and weight 913 ± 9 g) housed in concrete tanks gained 1450–2300 g after one year when fed diets with varying protein levels (Khan et al. 2004). Grass Carp fingerlings (12.78 ± 1.16 g initial weight) fed diets with varying chromium levels had a maximal weight gain of 480% (Liu et al. 2010), while cultured fingerlings (23.5–31.6 g initial weight) fed different types of weeds had a maximal weight gain of 1094%, SGR of 1.65%, and grew a maximum of 1.65 g/fish/day to attain final weights ranging between 35 and 270 g (Vinod et al. 2004, Majhie et al. 2006).

To evaluate any fishery, stock structure must be analyzed. To assess Grass Carp populations, standard length categories for size structure indices (based on maximum recorded length of 150 cm, Schofield et al. 2005) were proposed by Phelps and Willis (2013) to be: stock = 30 cm, quality = 54 cm, preferred = 68 cm, memorable = 89 cm, and trophy = 111 cm.

PHYSIOLOGICAL TOLERANCE

The broad temperature tolerance of Grass Carp (all life stages) is well established in the literature; the reported temperature tolerance range is 0–40 °C for fry and fingerlings, with a mean thermal maximum of 39.3 °C for adults and a temperature preference around 25 °C (Schofield et al. 2005). Grass Carp are abundant in sections of the Missouri River that exceed 30 °C every year (Aitkin et al. 2008).

Grass Carp is able to adjust to changing water temperatures by adjusting its respiratory responses, such as respiratory frequency, oxygen consumption rate, respiratory stroke volume, and gill ventilation, demonstrating a partial metabolic compensation to temperature (Zhao et al. 2011b). Numerous other studies have also investigated the effects of hyperthermia and hypothermia (e.g., Kuo and Hsieh 2006, Wu et al. 2012, Cui et al. 2013, 2014). However, these studies focused on the response and damage at the cellular level (e.g., cell viability, enzymatic activity, heat shock protein expression) to understand thermal compensation mechanisms, which is beyond the scope of this report and will, therefore, not be further addressed.

Grass Carp also tolerates a broad range of dissolved oxygen levels (Cudmore and Mandrak 2004), which is an important factor controlling growth. Low dissolved oxygen levels frequently occur in aquaculture ponds (generally $4 \text{ mg O}_2 \text{ L}^{-1}$), and Grass Carp can suffer hypoxic stress under these conditions (Yang et al. 2013a). Two studies in China assessed the influence of hypoxia and diet on growth under laboratory conditions. Gan et al. (2013) found that Grass Carp fed at low dissolved oxygen levels ($\sim 3 \text{ mg O}_2 \text{ L}^{-1}$) had reduced digestibility, appetite, feed efficiency, and growth performance compared to the high oxygen treatment ($\sim 6 \text{ mg O}_2 \text{ L}^{-1}$). Yang et al. (2013a) determined that increased levels of taurine in the diet resulted in increased hypoxia tolerance but did not alter growth performance under hypoxic conditions. Grass Carp juveniles held in fiberglass tanks survived acute hypoxia ($1 \text{ mg O}_2 \text{ L}^{-1}$, 28–29 °C) for ~ 65 min (control group, no taurine diet supplement) compared to ~ 75 min for those fed a high taurine diet (Yang et al. 2013a).

Heavy metals have been recognized as serious pollutants of the aquatic environment that can cause metabolic impairment. Numerous studies have investigated the influence and tolerance of Grass Carp to heavy metals. Naz and Javed (2013a) found that Grass Carp fingerlings chronically (12 weeks) exposed to a sub-lethal metal mixture concentration of zinc (Zn) and nickel (Ni) in aquaria had significantly lower weight gain than that of control fish. In another study, the toxicity level (mortality within 90 d of exposure) for Grass Carp exposed to a mixture of lead and Ni was assessed, and a mean 96-h LC_{50} of $56.42 \pm 2.51 \text{ mg} \cdot \text{L}^{-1}$ and a lethal

concentration of $120.98 \pm 7.18 \text{ mg} \cdot \text{L}^{-1}$ were found (Naz and Javed 2013b). A similar study, but with sub-lethal exposure to a metal mixture of Zn, Ni, and magnesium (Mg), obtained the same results (Naz et al. 2013). The effects of sub-lethal doses of copper on growth performance have also been studied, demonstrating that the 96-h LC_{50} of copper for juvenile Grass Carp was 1.717 ppm and the copper exposure resulted in significantly decreased final body weight, specific growth rate, food conversion efficiency, and survival in comparison to the control group (Nekoubin et al. 2012). In a lab experiment, the 96-h LC_{50} of juvenile Grass Carp was determined for acute levels of mercury, copper, cadmium, and zinc to be $0.23 \text{ mg} \cdot \text{L}^{-1}$, $0.09 \text{ mg} \cdot \text{L}^{-1}$, $18.47 \text{ mg} \cdot \text{L}^{-1}$, and $31.37 \text{ mg} \cdot \text{L}^{-1}$, respectively, and included changes in respiratory reaction (Wang et al. 2013a). In another study, the 96-h LC_{50} and lethal concentrations for 90-day-old Grass Carp was $5.17 \text{ mg} \cdot \text{L}^{-1}$ and $9.39 \text{ mg} \cdot \text{L}^{-1}$, respectively (Kousar and Javed 2012). Grass Carp exposed to the maximum aluminum concentration allowed in the aquatic environment ($0.1 \text{ mg} \cdot \text{L}^{-1}$) demonstrated oxidative stress and neurotoxic effects (Fernandez-Davila et al. 2012). Evidence for bioconcentration of aluminum in this study is worth noting, as Grass Carp is consumed by the human population and may constitute a hazard for human health. Exposure of Grass Carp fingerlings to sub-lethal concentrations of cadmium ($500 \text{ } \mu\text{g} \cdot \text{L}^{-1}$) resulted in significant reductions in growth due to reduced food intake, revealing that even very low concentrations of heavy metals like cadmium do cause effects on the growth of freshwater fish meant for human consumption (Ahmed et al. 2012). The 96-h LC_{50} of cadmium sulfate for Grass Carp was calculated as $9420 \text{ } \mu\text{g} \cdot \text{L}^{-1}$ and behavioural changes of fish subjected to different cadmium sulfate concentrations included respiratory difficulty, sudden jerking movement, and loss of balance (Yorulmazlar and Gül 2003). In another study, the acute toxicity of chromium (Cr) was determined for different age groups (60, 90, and 120 days) of Grass Carp (Shaukat and Javed 2013). Sensitivity varied with age; 60-day-old fish were most sensitive with a 96-h LC_{50} of $87.01 \text{ } \mu\text{g} \cdot \text{L}^{-1}$.

Finally, Grass Carp embryos and larvae exposed to an increased level of un-ionized ammonia ($0.879 \text{ mg} \cdot \text{L}^{-1}$) showed delayed embryonic development and reduced viability (Chen et al. 2012b). The hatch rate of embryos exposed to an increased $\text{NH}_3\text{-N}$ concentration was less than 70%, and viability of newly hatched larvae (24 h post-hatch) was only approximately 40% compared to the control, which had a >90% successful hatch rate and 97.8% viability of newly hatched larvae.

REPRODUCTION

The age at maturation, spawning cues, spawning duration, fecundity, fertilization rate and egg development of Grass Carp have been well studied and reviewed (Cudmore and Mandrak 2004, Schofield et al. 2005). In China, where the majority of this research has been carried out, recent literature has mainly focused on the effects of dams on Grass Carp spawning and early development, as spawning and nursery habitat in China has been altered in many regions, raising concern over the status of Grass Carp populations. See 'Conservation Status and Regulation' section for further detail on these studies.

To attain efficient and profitable practices, reproduction of Grass Carp has been well studied in the aquaculture industry. Extensive studies have been carried out on maximization of egg production, factors affecting hatching success and early development. These studies are not included in this report unless they contain information applicable to natural reproduction of Grass Carp.

Spawning periods typically range from late April or early May, end in late June or early July in the native range (Yangtze River) and are triggered by water temperature and hydrograph, with the latter believed to be the primary cue (Duan et al. 2009, Zhang et al. 2012, Kocovsky et al. 2012). The minimum flow increase needed to trigger spawning should last 1–2 days, with a daily

increase exceeding 300–500 m³/s but, if this increase is absent, a flash flood at the spawning grounds may also trigger Grass Carp to spawn (Wang et al. 2013b).

Although hydrograph is thought to be the primary cue, water temperature declines of 2–4 °C in March–May (a critical period for gonad development) were identified as the principle reason for observed spawning delays in the Yangtze River below the Three Gorges Dam, as timing of flow increase was not delayed (Wang et al. 2013b). The authors concluded that only if the cumulative temperature for gonad development and minimum temperature for onset of Grass Carp spawning occur, will flow increase produce a successful spawning event (Wang et al. 2013b). Furthermore, studies have shown that although spawning is clearly enhanced by an increase in discharge, such an increase is not required for some Asian carp spawning to occur (Kolar et al. 2007, Deters et al. 2013). However, in the Zhaoqing section of the Pearl River (south China) between 2006 and 2008, Grass Carp larvae peaked later than historically (larval peaks began in June, almost 1.5 months later than previously) despite water temperature levels remaining the same (21–23 °C); it was the hydrological regime that had changed (Li et al. 2008). These spawning delays have increased the risk of larval starvation, as zooplankton abundance was higher in summer than in autumn in the Pearl River estuary (Li et al. 2005). In a study on the egg presence and abundance in the middle Yangtze River, twelve predictor variables were included in a classification and regression analysis that showed that water temperature and the diurnal increase in water level were the two most significant factors for spawning activities (Li et al. 2013). In particular, spawning was favoured when water temperature was between 18 and 24 °C and coupled with the diurnal increase in water level greater than 0.55 m/d (Li et al. 2013).

In general, when the water temperature rises above 18 °C and water discharge increases, Grass Carp will be stimulated to spawn but spawning may occur without a change in discharge (Duan et al. 2009). If the water temperature drops below 18 °C, spawning activity will stop, with the optimal temperature for breeding being 21–24 °C (Duan et al. 2009, Wang et al. 2013b). The hydrological characteristics of the flow increase, such as the duration, rate of increase and timing, will also directly influence the corresponding larval abundance (Yi et al. 2010).

Other cues of spawning were investigated by Wang et al. (2010). In China, the relationships between meteorological conditions (wind, rainfall, temperature, air pressure, sunshine hours, and humidity) and natural spawning behaviour were assessed and the results showed that the spawning activities were most likely to be activated in consecutive rainy days or days when weather changed drastically. Furthermore, the authors conclude that the average rainfall in the initial spawning days is higher than that in the actual spawning time windows. However, Li et al. (2013) found no influence of weather on initiation of spawning behaviour.

Spawning times of Asian carps in the lower Missouri River were estimated based on developmental stage, temperature and water velocity; spawning rate was determined to be higher during the daytime between 05:00 and 21:00 h than at night and larvae determined to be spawned from areas of high sinuosity (Deters et al. 2013). Unlike the Yangtze River, spawning sites in the lower Missouri River were not limited to a few sites; the river is highly modified and turbulent, which likely offers numerous sites for adequate spawning (Deters et al. 2013). No evidence of substantial spawning in tributaries or tributary confluences was found (Deters et al. 2013). However, Grass Carp larvae only represented 2.3% of the collected Asian carp larvae in this study so caution should be taken when interpreting these results specifically for Grass Carp.

Studies in the United States estimate spawning to occur in late April to early June in the Red and Washita rivers (Hargave and Gido 2004), May through June in the lower Missouri River (Deters et al. 2013) and, based on temperatures, spawning has been predicted to start June 23

± 7.5 d in western Lake Erie and end approximately September 15 (Kocovsky et al. 2012, Chapman et al. 2013).

In a set of experiments carried out in Turkey during Grass Carp spawning season, Bozkurt and Ögretmen (2012) reported an egg size and fecundity of female Grass Carp of 1.04 ± 0.028 mm and $417,867 \pm 36,274$ egg/fish, respectively. The fertilization capacity of sperm was tested with the same egg pool and fertilization rate was determined as mean $79.3 \pm 2.95\%$ and was positively correlated with sperm motility, egg size, and fecundity. Size of water-hardened eggs is related to temperature and maternal size, with larger eggs coming from larger females and from warmer temperatures (George and Chapman 2015).

After Grass Carp eggs are released and fertilized, the vacuole is broken and fluid is released, which then allows water to enter the egg membrane, causing the egg to expand (Chapman and Wang 2006). The semi-buoyant eggs of Grass Carp develop to hatching while drifting in river currents and will not likely survive if they fall to the bottom (George and Chapman 2015). As such, Grass Carp eggs are considered to require discernible current that creates turbulence to keep them afloat. Due to these flow requirements, unobstructed stretches in large rivers of 28–100 km are typically considered necessary for Asian carp eggs to successfully develop (George and Chapman 2015), along with a water velocity exceeding 0.7 m/s (Kocovsky et al. 2012).

Based on having summer temperatures >21 °C (for rapid incubation of eggs) and at least 100 km of passable river, Kocovsky et al. (2012) concluded that the Maumee, Sandusky, and Grand rivers were the most likely to support spawning of Asian carps in Lake Erie. In a similar study, Mandrak and Cudmore (2004) identified 41 Canadian tributaries to the Great Lakes that were unimpounded from the river mouth to at least 100 km upstream and would, therefore, be suitable tributaries for Asian carp spawning. Sixteen of these were in the Lake Superior basin, 14 in Lake Huron, and five in the Erie basin and eight in the Ontario basin. However, the exact length of river required for eggs to successfully develop likely depends on other factors as well, such as turbulence and temperature (George and Chapman 2015). Predicting the number of suitable spawning tributaries is important for determining the probability of Grass Carp establishment in the Great Lakes.

Using river hydrodynamics, water temperature and egg development dynamics, Garcia et al. (2013, 2015) developed the Fluegg model, an assessment tool, to predict suitable spawning tributaries for recruitment. A simulation of Asian carp (Silver Carp) eggs in the Lower Saint Joseph River, a tributary of Lake Michigan, revealed that the eggs at risk of hatching ranged from 0–93% depending on river conditions. The most critical condition (highest percentage of eggs at risk of hatching) occurred at the lowest discharge and at peak water temperatures. Overall, this simulation showed that eggs can hatch successfully in the Lower Saint Joseph River under a broad range of hydrodynamic conditions for temperatures greater than 23 °C in a river reach that is about 40 km long; much shorter than the 100 km previously assumed to be adequate based on native conditions (Kolar et al. 2007, Kocovsky et al. 2012).

Similar results were found in another U.S. study that investigated four Great Lakes tributaries: two Lake Michigan tributaries (the Milwaukee and St. Joseph rivers) and two Lake Erie tributaries (the Maumee and Sandusky rivers) to determine if these tributaries could be potential spawning grounds based on hydraulic and water-quality characteristics that allow successful spawning and transport of Asian carp eggs (Murphy and Jackson 2013). They found that all four tributaries exhibited potential settling zones for Asian carp eggs both within the estuaries and river mouths and within the lower 100 kilometers (km) of the river. The impoundments created by many of the larger dams on these rivers acted to sufficiently decelerate the flows and allowed the shear velocity to drop below the settling velocity for Asian carp eggs, which allowed the eggs to fall out of suspension and settle on the bottom where it is thought the eggs would

perish. Only St. Joseph and Maumee rivers both had extensive settling zones (>5 km) behind major dams. While hydraulic data from all four rivers indicated settling of eggs is possible, all four exhibited sufficient temperatures, water-quality characteristics, turbulence, and transport times outside of settling zones for successful suspension and development of Asian carp eggs to the hatching stage before the threat of settlement (Murphy and Jackson 2013).

The embryonic and larval development of Grass Carp is influenced by temperature (Yi et al. 2006, George and Chapman 2015). At an experimental water temperature of 18–24.2 °C, larvae hatched in about 37 h post-fertilization at a length of 6 mm (Yi et al. 2006) but, in an experiment using a cold (19–19.21 °C) and warm (22.38–22.75 °C) water treatment that differed by less than 3 °C, a 16–17 h difference in hatching time resulted and a nearly three-day difference in time to gas bladder inflation was reported (George and Chapman 2015). The critical thermal minimum for embryonic stages was 13.5 °C and 13.3 °C for larval stages (George and Chapman 2015). In another study, based on the evaluation of larval development, growth and survival, the optimal temperature for embryonic development was determined to be 32 °C, and temperatures below 20 °C were reported to be too low for the proper development of Grass Carp (Korwin-Kossakowski 2008). From the middle Yangtze River, Jiang et al. (2010) reported that the hatching time of Grass Carp is approximately 30–35 h at 20–23 °C. In the Yangtze River below the Three Gorges Dam, Grass Carp larvae were hatched between May 31 and July 9 (Zhang et al. 2012).

Embryonic development and growth are also influenced by oxygen availability. In a study to understand the underlying effects of hypoxia on cellular and molecular mechanisms, Sun et al. (2011) found that hypoxia caused significant developmental delay and growth retardation during embryogenesis due to overexpression of insulin-like growth factor binding protein 1. Both the somite number and body length was lower in hypoxic conditions (1.0 ± 0.5 mg/L) compared to normoxic conditions (7.0 ± 0.5 mg/L) at ~22 °C (Sun et al. 2011).

Grass Carp larvae must reach nursery habitats, such as inundated vegetation, soon after hatching to avoid predation and obtain food (Hargave and Gido 2004). Detailed criteria for Grass Carp nursery habitat are lacking; Hargave and Gido (2004) found no difference in littoral habitat characteristics between sites with and without Grass Carp larvae in the Washita River.

In general, larvae and juveniles move from the mainstem of rivers into floodplain lakes for feeding. River-lake migrations of Grass Carp in the Dongting Lake and Yangtze River (China) were investigated from March–December (Ru et al. 2013). In this area, flooding occurs in March–August. Sampling revealed that Grass Carp only occurred in the lake during July–November and peaked in July and August, with samples mainly composed of 0+ fishes. No larvae or juveniles were found in the lake prior to this time, which suggests that they drift downstream and feed in the mainstem until they have the swimming ability to migrate into the lake. These results suggest that the key time for migration into the lake for juveniles occurs July–August. The exact time that adults leave the lake was not determined due to overfishing, but this study suggests that massive migration of young fish into the lake occurs in July–August (Ru et al. 2013).

In an experiment, Grass Carp larvae at the gas-bladder emergence stage were found to exhibit a very strong positive phototactic response and young larvae exhibited upward and downward swimming, interspersed with long periods of lying on the bottom (George and Chapman 2015). Swimming capacity increased with ontogeny and larvae were capable of horizontal swimming and holding position with gas-bladder emergence (George and Chapman 2015). In the Yangtze River, there was a slightly higher drift density of larvae after sunrise and before sundown (Jiang et al. 2010).

As previously mentioned, reproductively sterile Grass Carp have been produced through the induction of triploidy (three sets of chromosomes). Induced polyploidy is attained by applying

temperature- or pressure-shock to the eggs, inhibiting the second maturation division of meiosis in the fertilized egg, thereby, causing retention of the extra chromosome set contained in the second polar body of the ovum (Cassani et al. 2008). This process causes the triploid condition in Grass Carp giving them a chromosome number of 72 (3N) instead of the natural 48 (2N) and makes them functionally sterile. However, this process is not 100% effective (e.g., 5% of treated Grass Carp were diploid; Papoulias et al. 2011) and some triploid carp have been shown to produce viable gametes and offspring (Papoulias et al. 2011). It has been predicted that triploids could reproduce in extremely limited numbers if a mature diploid population and ideal spawning habitat were present. Even with reduced sperm production and quality, the triploid male may be capable of mating with a diploid female as if triploid males do exhibit spawning behaviour, they can spermiate naturally and successfully inseminate normal eggs (Cassani et al. 2008).

FEEDING AND DIET

Grass Carp feeding preferences have been investigated for all life stages (Cudmore and Mandrak 2004, Schofield et al. 2005), particularly with respect to the use of Grass Carp in aquaculture and to control aquatic weeds (Cassani et al. 2008). In general, Grass Carp are reported to most commonly feed on Hydrilla (*Hydrilla verticillata*) and pondweeds (*Potamogeton* spp.) and the most commonly avoided macrophytes are reported in the genera *Nymphaea*, *Potamogeton*, *Myriophyllum*, *Nuphar*, and *Nypha*; however, feeding preference changes under different environmental conditions (Dibble and Kovalenko 2009).

In Iran, Grass Carp is used to control dense stands of submerged and free-floating weeds. In a feeding-preference study, Filizadeh et al. (2007) found that Grass Carp (45–70 g) in large outdoor tanks (25 ± 0.05 °C) fed preferentially on 10 aquatic plants in the following order: *Lemna minor*, *Chara* sp., *Najas guadalupensis*, *H. verticillata*, *Potamogeton pectinatus*, *P. perfoliatus*, *P. crispus*, *Azolla filiculoides*, *Ceratophyllum demersum*, and *Myriophyllum spicatum*. The soft and tender plant tissue, such as young leaves, was selected by smaller fish, whereas, bigger fish fed on a wide variety of tough and fibrous plants.

In another plant-selectivity experiment, Dorenbrosch and Bakker (2012) presented five submerged macrophyte species (*Callitriche* sp., *Chara globularis*, *Elodea nuttallii*, *Myriophyllum spicatum*, and *Potamogeton pectinatus*) to Grass Carp (21.8–324.7 g). Grass Carp fed preferentially on *Potamogeton pectinatus* and *Callitriche* sp., whereas, *Myriophyllum spicatum* was the least consumed and also had the highest phenolic concentration. However, when presented with animal prey (*Gammarus pulex*) and the most palatable macrophyte (*Potamogeton*), Grass Carp preferred the animal prey.

A feeding preference study of triploid Grass Carp fingerlings (8.3–11.8 cm in length) in water found that Grass Carp avoided eating creeping water primrose *Jussiaea repens* and buttercup *Ranunculus longirostis* (Murphy et al. 2002). When water buttercup was presented as the sole vascular plant food source, Grass Carp either did not eat, or consumed the filamentous algae *Spirogyra*. The authors documented lesions in the mouth, pharynx, and intestines of Grass Carp that were tube-fed aquatic buttercup filtrate. The toxic effect of this plant likely explains why Grass Carp avoided consuming it, although the authors suggest that water primrose may simply be unpalatable. Identification of plants that Grass Carp avoid eating may help increase the effectiveness of aquatic amphibian habitat rehabilitation (Murphy et al. 2002).

In Georgia, lab feeding experiments were carried out to determine if Grass Carp had a preference for native plants (33 species) or exotic plants (14 species) collected from sites where species were found growing sympatrically in the surrounding environment (sites in Georgia, South Carolina, and Florida, U.S.) (Parker and Hay 2005). Parker and Hay (2005) presented macrophytes in random order to juvenile Grass Carp contained in buckets with 3–5 individuals,

as Grass Carp would not feed when kept individually. The mean percentage of Grass Carp feeding on all native and exotic macrophyte species did not differ. The authors suggest that the lack of preference may be partially explained by the lack of shared evolutionary history with most of the native and exotic species presented.

The diet of Grass Carp may also vary seasonally. The seasonal diet composition of Grass Carp held in earthen fish ponds (depth range of 1.5–2.0 m) in Egypt was assessed by removing digestive tracts and analyzing the gut content (el-Deeb and Ismail 2004). Based on the index of relative importance (IRI), available food items (shell fragments, snail soft body, artificial food, insect parts, fish scales, plants, and unknown) varied by season; in the summer, shell fragments were the main food item, whereas, in the spring and autumn, artificial fish food was the most important food item. During winter, the stomachs of most fish samples collected were empty or only had traces of food.

The occurrence of plants in the diet tends to increase approximately three weeks after hatching (Cudmore and Mandrak 2004). To determine the diet of fry and at what size fry change their feeding habits from an omnivorous to herbivorous diet, gut contents of stocked Grass Carp fry (0.04 ± 0.01 g, 1.48 ± 0.03 cm) in earthen ponds ($20.41\text{--}23.5^\circ\text{C}$) were analyzed every week for 12 weeks (Kirkagaç 2003). During the first week, animal material represented 74% of the gut contents, and from the second week onwards, the proportion of plant material was higher (mean 79%) than the animal content. In the seventh week, when Grass Carp reached 4.83 ± 0.09 cm, filamentous algae were replaced by macrophyte fragments. Besides the macrophytes, animal material consisted of zooplankton (Rotifera and Cladocera) and benthic fauna, with trace amounts of chironomidae larvae.

As a herbivore, Grass Carp has the ability to digest aquatic macrophytes, but the sources of cellulase and cellulase-producing bacteria in fish digestive tracts have not been clearly identified (Jiang et al. 2011). Fishes are generally considered unable to produce endogenous cellulase and some reports have shown that cellulase activity resulted from ingested food. However, analysis of digestive tracts from adult Grass Carp (2.001 kg) starved for 10 days revealed that cellulase activity is at least partially accounted for by bacteria of *Aeromonas*, which are indigenous species in the gut of Grass Carp (Jiang et al. 2011). In addition, the differential feeding patterns of Grass Carp fed with plant and animal diets has been considered to represent an adaptation to herbivory that enables Grass Carp to achieve high growth rates on plant material with relatively poor nutritional quality; however, little information is available on the physiological and molecular basis for this feeding strategy (He et al. 2013). In one study, Grass Carp (1.81 ± 0.42 g) were maintained in ponds and fed a plant (*Lemna minor*) or animal diet (*Chironomus tentans*) for 60 days; gut contents were analyzed at the food transition stage from zooplankton or benthos to aquatic macrophytes. Fish fed the plant diet had significantly higher gut growth in terms of length and weight and had up-regulated expression of neuropeptides and leptin receptors as well as trypsin and amylase to increase the intake and digestion of plant food (He et al. 2013).

HABITAT

Grass Carp has been one of the most important traditional domestic freshwater aquaculture fish in China. Its habitat includes lakes, ponds, pools, and backwaters of large rivers, but it is most abundant in Yangtze River and its adjacent lakes (Liao et al. 2005, Ru and Liu 2013). In general, Grass Carp prefer large, slow-flowing, or standing waterbodies with vegetation and require strong current for successful spawning. Juveniles typically use nursery areas in floodplain backwaters, reservoirs, and lakes; Grass Carp may generally winter in deeper water (USGS 2015).

A few recent studies investigated the habitat use of Grass Carp in areas it has invaded in North America. One study (Stich 2011) of adult Grass Carp stocked in Lake Gaston (North Carolina and Virginia) used telemetry to investigate habitat use (water depth and distance to shore) between seasons of 101 radio-tagged Grass Carp (264–573 mm, TL) for up to 2 years. After stocking, Grass Carp initially were found most often in small creeks and backwaters near stocking areas and moved little until their second spring. At age 2, all Grass Carp moved out of the small creeks and were found throughout the main lake. Grass Carp occupied shallow water in Lake Gaston at a mean depth of 2.9 m, but the depth of water at Grass Carp locations varied with season. Grass Carp were found in the deepest water (~3.4 m) in winter and in the shallowest water (~2.5 m) in the summer; as such, the depth of Grass Carp locations was strongly determined by water temperature. The depth of Grass Carp locations also varied with age; age-2 fish were found in shallower water depths than age-1 fish. Grass Carp were located a mean distance of 40 m from the nearest shore throughout the year in Lake Gaston and were found significantly further from the shore when water temperature was high, holding all other factors constant. The findings from this study suggest that the habitat use of Grass Carp changes with season and may change with age, but fish continue to use areas where submerged aquatic vegetation occurs.

In another study, Illinois River and sites in the Missouri basin were sampled and the habitat from which Grass Carp juveniles were collected was described (C. Hayer, USGS, pers. comm.). Preliminary results suggested that the presence of juvenile Grass Carp was associated with open water and then by vegetated (terrestrial, emergent and submergent) habitats. It is unclear as to whether there is any association with water depth, as all sites were relatively shallow. Finally, sampling for juvenile Asian Carp from sites in the Mississippi River, Missouri River, and La Grange Reach of Illinois River revealed that in sites where Grass Carp were found, they were generally located at a mean water depth of ~45 cm and, in sites where Grass Carp were absent, the mean water depth was ~55 cm. The depth location was not significantly different for the presence/absence of Grass Carp juveniles, but juveniles were found in shallower water than the larvae (C. Hayer, USGS, pers. comm.).

INTERSPECIFIC INTERACTIONS

No study has examined predation in North America by fishes or birds on Grass Carp juveniles. However, there is some information from the aquaculture industry as to the general predators of Grass Carp in these facilities. For example, the South Carolina Department of Natural Resources (SC DNR) listed a number of potential predators that can seriously reduce or eliminate Grass Carp: Largemouth Bass, Bowfin, Osprey, herons, otters, and alligators (SC DNR 2014). The main impact of predators occurs on young Grass Carp as they prefer shallow water for feeding and are easily seen swimming in small groups or individually at the surface of ponds (SC DNR 2014). In Alberta, the Northern Pike is listed as the most likely predator of concern for Grass Carp stocked in ponds (Alberta Agriculture Research Division 2015). Potential predators of stocked Grass Carp in Lake Gaston, Florida include Striped Bass (*Morone saxatilis*), Blue Catfish (*Ictalurus furcatus*), and Flathead Catfish (*Pylodictis olivaris*) (Stich 2011). In Croatia, Grass Carp ponds provide Great Cormorant (*Phalacrocorax carbo sinensis* L.) with highly suitable nesting, feeding, and resting places. Grass Carp were found to represent 11.6% of the cormorants' diet, which is in accordance with their composition in the pond; thus, cormorants appear to pose a predation threat to Grass Carp (Opačak et al. 2004). In the Great Lakes, there are a number of piscivorous fishes that could potentially feed on juvenile Grass Carp (Table 3) and a number of fishes that may prey upon Grass Carp eggs, but given the spawning behaviour of Grass Carp, it is more likely that pelagic river fishes would consume Grass Carp eggs, than benthic and lake fishes. Predation on adult Grass Carp in the Great Lakes would most likely come from humans and large predatory birds and not from piscivorous

fishes, due to the rapid growth rate of Grass Carp and the gape-limitation of piscivorous fishes (Table 3).

Table 3. Potential predators of Grass Carp in the Great Lakes basin.

Prey on Larval (< 20 mm) Grass Carp	Prey on Juvenile (20–200 mm) Grass Carp	Prey on Sub-adult and Adult > 200 mm Grass Carp
Alewife (<i>A. pseudoharengus</i>)	Birds (e.g., Egrets, Cormorants, Herons)	Humans
White Bass (<i>M. chrysops</i>)		Large predatory birds (e.g., Bald Eagle, Osprey, White Pelican)
Round Goby (<i>N. melanostomus</i>)	Largemouth Bass (<i>M. salmoides</i>)	
Tubenose Goby (<i>P. semilunaris</i>)	Rock Bass (<i>A. rupestris</i>)	Piscivorous fishes (predation limited on adult Grass Carp due to gape limitation):
White Perch (<i>M. Americana</i>)	Smallmouth Bass (<i>M. dolomieu</i>)	Muskellunge (<i>E. masquinongy</i>)
	White Bass (<i>M. chrysops</i>)	Northern Pike (<i>E. lucius</i>)
	Bowfin (<i>A. calva</i>)	
	Black Bullhead (<i>A. melas</i>)	
	Brown Bullhead (<i>A. nebulosus</i>)	
	Yellow Bullhead (<i>A. natalis</i>)	
	Burbot (<i>L. lota</i>)	
	Channel Catfish (<i>I. punctatus</i>)	
	Black Crappie (<i>P. nigromaculatus</i>)	
	White Crappie (<i>P. annularis</i>)	
	Freshwater Drum (<i>A. grunniens</i>)	
	Longnose Gar (<i>L. osseus</i>)	
	Spotted Gar (<i>L. oculatus</i>)	
	Muskellunge (<i>E. masquinongy</i>)	
	Trout Perch (<i>P. omiscomaycus</i>)	
	White Perch (<i>M. americana</i>)	
	Yellow Perch (<i>P. flavescens</i>)	
	Northern Pike (<i>E. lucius</i>)	
	Green Sunfish (<i>L. cyanellus</i>)	
	Northern Sunfish (<i>L. peltastes</i>)	
	Orangespotted Sunfish (<i>L. humilis</i>)	
	Pumpkinseed (<i>L. gibbosus</i>)	
	Walleye (<i>S. vitreus</i>)	
	Warmouth (<i>Lepomis gulosus</i>)	

Most research on interspecific interactions between Grass Carp and other species has examined the indirect effects of Grass Carp through macrophyte consumption and the subsequent changes to zooplankton and other fish species (see section 'Recorded Impacts Associated with Introduction').

BEHAVIOUR AND MOVEMENTS

The movement of Grass Carp has been reviewed as it relates to spawning and early development (Cudmore and Mandrak 2004); see 'Reproduction' section.

In the native range in Asia, migration behaviours have been disrupted due to river impoundment, causing alterations in timing of environmental triggers such as flooding and low

flow (Xie et al. 2007) and loss of spawning habitat (Yi et al. 2010). For example, egg maturation may now occur asynchronously with upstream spawning runs in response to flooding, reducing spawning success. Migration back to main channels from feeding grounds in response to low flow conditions may now occur before energy has been stored sufficiently for the overwintering period (Xie et al. 2007).

In North America, there have been a few studies on Grass Carp movement. In a large impoundment in Arkansas, triploid Grass Carp were tagged and released and relocated semi-monthly during a 12 month period (Olive et al. 2010). Of the 48 tagged fish, 39 (82%) were consistently located in the reservoir while one fish moved upstream and then returned and five fish remained upstream of the reservoir in the Ouachita and Saline rivers. The average home range movement was 575 ha and maximum movement from the release site averaged 5.7 and 51.5 km for Grass Carp that remained in and left the reservoir, respectively. Movement was greatest during the fall with an average daily movement of 238 m/d. In another study in Lake Gaston (North Carolina and Virginia), movement of tagged Grass Carp released for Hydrilla control were followed for two years (Stich 2011). The average rate of movement for Grass Carp (333–467 mm, TL) was about 137 m/d, with rapid dispersal after stocking followed by long periods of no movement. When time after stocking was held constant in models of behaviour, fish moved about 200 m/d more in the second year after stocking than in the first year (Stich 2011).

Wilson (2014) compared rates of expansion in the Mississippi and Illinois rivers with their tributaries. Grass Carp began to expand rapidly, in the mainstem and tributaries, after 25 years of lag but sampling in first- through fourth-order streams along the La Grange Reach of the Illinois River produced only five Grass Carp. Cumulative frequency distribution analysis suggests that geographic expansion of Grass Carp in tributaries of the Illinois and Mississippi rivers is in an early stage and likely still increasing (Wilson 2014).

As previously mentioned, an electric barrier in the Chicago Sanitary and Ship Canal acts to impede fish dispersal between the Great Lakes and the Mississippi River basin. The barrier is a micro-pulsed, graded DC electric field that is strongest near the centre and weak around the edges. In this way, fishes can sense the electric field before they are stunned, and are repelled (Stainbrook et al. 2007). Due to concern over Common Carp passage through the barrier, the electric field was increased by 50% and this new level seems to have been effective at preventing upstream movement of adult Common Carp (Sparks et al. 2011). In the Central Arizona Project canal, two electric fish barriers were installed, one in the South Canal and one in the Arizona Canal (Clarkson 2004). The effectiveness of these electric fish barriers was reviewed as Grass Carp were captured above the South Canal electrical barrier, with no prior barrier failure reported; and, a similar situation has occurred in the Arizona Canal (Clarkson 2004). It was acknowledged that some fishes are capable of traversing a fully operational electrical barrier during low-flow conditions.

Otolith microchemistry can also be used to determine movement of fish as otolith chemistry reflects the chemical composition of the water and surrounding habitat. For example, otolith chemistry has been used to discern from which rivers (e.g., Sandusky River, Missouri River) Grass Carp have originated (Chapman et al. 2013, Whittedge 2014).

Two studies assessed swimming behaviour and metabolism of Grass Carp. The first study found swimming performance of Grass Carp increases with temperature and the critical swimming speed (i.e., the water speed at which Grass Carp can no longer maintain its position or its maximal sustainable speed) was found to be 33.1 ± 1.1 cm/s and 43.2 ± 1.7 cm/s at 15 °C and 25 °C, respectively (Yan et al. 2012). In a study by Cai et al. (2014), the relationship between feeding and swimming of juvenile Grass Carp was assessed; swimming efficiency

increased after digestion was complete and decreased with extended food deprivation. Anaerobic metabolism began at swimming speeds 28.3 to 40.2% of critical swimming speed and decreased with time after feeding. The authors concluded that feeding and food deprivation affects swimming efficiency, metabolism and swimming capability.

DISEASES AND PARASITES

A large number of disease-causing organisms are known to infect Grass Carp (Cudmore and Mandrak 2004). Numerous studies have been conducted on disease prevention for Grass Carp as it is one of the most economically valuable fishes in aquaculture and the food industry (Cassani et al. 2008, Liu et al. 2009). For the purposes of this report, studies that identify diseases, viruses, and parasites of Grass Carp are included, but the treatment of and specifics (e.g., genome structure and genetic diversity; Zhang and Gui 2015) of disease-causing agents are beyond the scope of this report and are not discussed.

Fish-borne zoonotic trematodes (FZTs) in cultured Grass Carp are prevalent in many different countries. These include liver and intestinal flukes, which may infect mammal- or bird-definitive hosts, including humans, and represent a significant public health problem worldwide (Chi et al. 2008). In Iran, a number of non-native *Dactylogyrus* spp., which are trematodes infecting cyprinid gills, have been introduced to various waterbodies with the introduction of Grass Carp; some of these trematodes have been reported to cause high mortalities in fry and fingerling production (Shamsi et al. 2009). Metacercariae of the vitreous humor parasite species *Tylodelphys clavata* were also observed in Grass Carp collected from fresh and brackish waters of Iran (Barzegar et al. 2008). Sampling of Grass Carp ($n = 148$) in northern Vietnam revealed a 62.8% prevalence of FZTs in nursery pond samples and a 61% FZT prevalence in grow-out ponds with five different trematode species recovered; these values represented the highest prevalence of all seven cultured fish species tested (Chi et al. 2008). Another study from northern Vietnam also found that the FZT prevalence (four species) in cultured Grass Carp juveniles was higher than that of all other carp species, with a prevalence of 14.1% in the first week and up to 57.8% after overwintering, indicating that some transmission of FZTs occurs during the winter (Phan et al. 2010a). In another study, no significant difference in the prevalence of FZTs was found between wild-caught fish and fish from ponds in Red River Delta, Vietnam; FZT prevalence in Grass Carp was 82.7%, with the most common intestinal fluke being *Haplorchis pumilio* (Phan et al. 2010b). The prevalence of FZTs in fish fry and juveniles from fish farms in Vietnam tend to also show seasonal variation with maximal prevalence in the rainy season (June–November) (Thien et al. 2009.) Grass Carp can also host the trematode *Clonorchis sinensis*, which can subsequently be transmitted to humans (Chen et al. 2010). Infection rates in Guangdong province in China, especially in the Pearl River Delta region, are relatively high amongst people. The infection rate of metacercariae in Grass Carp in this study reached 52.42% and the degree of infection in Grass Carp was the highest of all tested species, making it the most important host for the parasite (Chen et al. 2010). In Serbia, metacercariae from *Posthodiplostomum cuticola* (agent of black spot disease) were isolated from infected Grass Carp in a fish pond for the first time; although infection of Grass Carp in the wild in Serbia had been previously documented.

The first record of the Asian fish tapeworm (*Bothriocephalus acheilognathi*), a potentially serious pathogen, in the Changjiang River drainage (China) was reported in Grass Carp obtained from a fish farm in the main tributary of the river in May 2006 (Xi et al. 2011). The Asian fish tapeworm was first reported in the U.S. in 1975 and was most likely introduced with Grass Carp; since its introduction it has spread and established in native fishes in numerous states (Choudhury et al. 2006). The range now extends to include Wisconsin/Michigan, possibly

Colorado, and most notably, Manitoba, Canada (which expands the most northern range of this species).

In the Danjiangkou Reservoir in central China, Grass Carp has recently been identified as a new host for the parasitic nematode *Camallanus cotti*, which was originally reported from freshwater fishes of Japan (Wu et al. 2007). In this study, the prevalence of *C. cotti* varied seasonally and was most prevalent in Grass Carp in May (100%) (Wu et al. 2007). Epitheliocystis is an infectious disease caused by a bacterium belonging to the order *Chlamydiales* and was identified for the first time in cultured Grass Carp in Austria (Kumar et al. 2013).

Hemorrhagic disease, caused by Grass Carp reovirus (GCRV), is one of the most serious infectious diseases of Grass Carp and causes significant mortality of juveniles (Jiang 2009). The optimal epidemic temperature of this disease is 25–28 °C (Jiang 2009). An aquareovirus not closely related to other members of the species, termed 'American Grass Carp reovirus' was isolated from several fish species in the U.S. and was implicated in a winter die-off of Grass Carp fingerlings on a commercial farm in Arkansas in 2005 (Jaafar et al. 2008).

Koi herpes virus (KHV) can cause mass mortality in Common Carp and several outbreaks have occurred in the U.S. The virus may remain dormant and inactive over long periods of time, but can be reactivated and become pathogenic again (Radosavljevic et al. 2012). Fish often develop in polyculture, which presents an opportunity for exposure of Grass Carp to Common Carp or Koi that may be KHV carriers. Although Grass Carp is not considered to be susceptible to this virus, a recent study in Belgrade identified that CyHV-3 was present in the organs of Grass Carp after being held in tanks with infected Common Carp, suggesting that CyHV-3 may cause latent infection and has the potential to infect a broader host range than previously thought (Radosavljevic et al. 2012). Similar findings of the horizontal transmission of KHV in polyculture were observed in Poland, but from Grass Carp to Common Carp (Kempter et al. 2012).

Preventing movement of fish viral pathogens like KHV, spring viremia of carp virus (SVCV), and GCRV in a global environment is of high importance; surveillance of Cambodia, Lao PDR, Myanmar, Philippines, and Vietnam indicated that these three viral pathogens are not yet present in these five countries, although there have been detections in the surrounding regions (Lio-Po et al. 2009).

Zheng et al. (2012) identified multiple strains of *Aeromonas hydrophila* from cultured Grass Carp suffering from septicemia in China. The authors highlight that the multi-infection of this important pathogen may be an emerging threat in Grass Carp farming and food safety.

Avian vacuolar myelonopathy (AVM) is an often-lethal neurologic disease that affects water birds and their avian predators, and is caught by eating submerged aquatic vegetation (SAV) that is covered by a toxin-producing cyanobacterium (Haynie et al. 2013). In this study, Grass Carp fed covered SAV developed lesions, but chickens fed infected Grass Carp tissue showed no neurologic signs, suggesting that the risk to piscivorous avifauna is likely low; however, studies of longer exposure are necessary (Haynie et al. 2013).

In the Great Lakes and Mississippi River basins, the National Wild Fish Health Survey has not found any evidence of the target pathogens and parasites of national concern (e.g., SVCV, *Aeromonas salmonicida*, viral hemorrhagic septicemia virus) in Grass Carp captured from 1996 to present (USFWS 2015).

RECORDED IMPACTS ASSOCIATED WITH INTRODUCTION

GENERAL

Numerous studies have documented the biotic and abiotic alterations to ecosystems due to the introduction of Grass Carp, and various authors have reviewed the literature on Grass Carp and discussed the potential impacts caused by the introduction of this species. In general, the introduction of Grass Carp has been linked to changes, either directly or indirectly, to aquatic macrophytes, water quality, and aquatic fauna, including plankton, benthic macroinvertebrates, fishes, waterfowl, and amphibians; however, the effects tend to be inconsistent, suggesting that the effects of Grass Carp are complex and depend on multiple factors (Cudmore and Mandrak 2004).

Pípalová (2006) summarized the state of knowledge of the effects of Grass Carp on waterbodies based on a selected literature review of aquatic plant control and consequences of its introduction, including impacts on water and sediment chemistry, and the phytoplankton, zooplankton, zoobenthos, fish, amphibian, and water bird communities. Primary consequences of Grass Carp feeding include a decrease or elimination of aquatic plant biomass and the release of nutrient-rich excrement into the water, resulting in subsequent water quality changes (Pípalová 2006). However, the effects are highly variable and often inconclusive due to lack of rigor in the studies conducted to date. The same conclusion is drawn for effects on phytoplankton, zooplankton, zoobenthos, and fishes. For example, the abundance of Northern Pike declined or was eliminated after Grass Carp removed all vegetation, but with no control, it remains unclear as to the mechanism and role of Grass Carp in this change (Pípalová 2006).

Cassani et al. (2008) summarized biological and ecological information concerning triploid Grass Carp and its use to manage aquatic plants, including the effects on waterfowl habitat, fish communities, water quality, phytoplankton, zooplankton, sediment chemistry, and benthic invertebrates. Much of the same literature is reviewed as that in Pípalová (2006). Cassani et al. (2008) similarly concluded that stocking density, plant selectivity, Grass Carp age, temperature conditions, and quality of food present are all important factors influencing the amount of aquatic plants consumed and the subsequent effects.

Dibble and Kovalenko (2009) reviewed the literature to determine whether previous studies addressed ecological impacts and their underlying mechanisms. The review yielded >1000 studies, but data on ecological interactions and effects on habitat complexity or community-structuring processes were very limited. Fewer than 50 citations addressing Grass Carp impacts referred to 'ecology' and none validated causal mechanisms. The authors concluded that the current knowledge was not sufficient to accurately predict the long-term effects of Grass Carp on freshwater ecosystems, as the majority of studies focused on the biology of the introduced Grass Carp and eradication success of aquatic plants.

Recently, Wittmann et al. (2014) reviewed and evaluated the experimental evidence available on the ecological impacts of Grass Carp using meta-analysis. The authors conducted a fixed-effects model meta-analysis to examine the direct and indirect ecosystem effects of Grass Carp, including both biotic impacts on macrophytes, invertebrates, fish, amphibians, and birds, as well as abiotic impacts on dissolved oxygen, turbidity, nutrients, and pH. Of 193 studies, 18 experimental studies dealt with Grass Carp impacts. Grass Carp had a significant negative effect on biota, which was driven primarily by the reduction in biomass/abundance of macrophytes (native and non-native), and a negative effect on amphibians. Grass Carp had a positive effect on abiotic factors (all abiotic factors aggregated), which was mainly driven by turbidity (Figure 11).

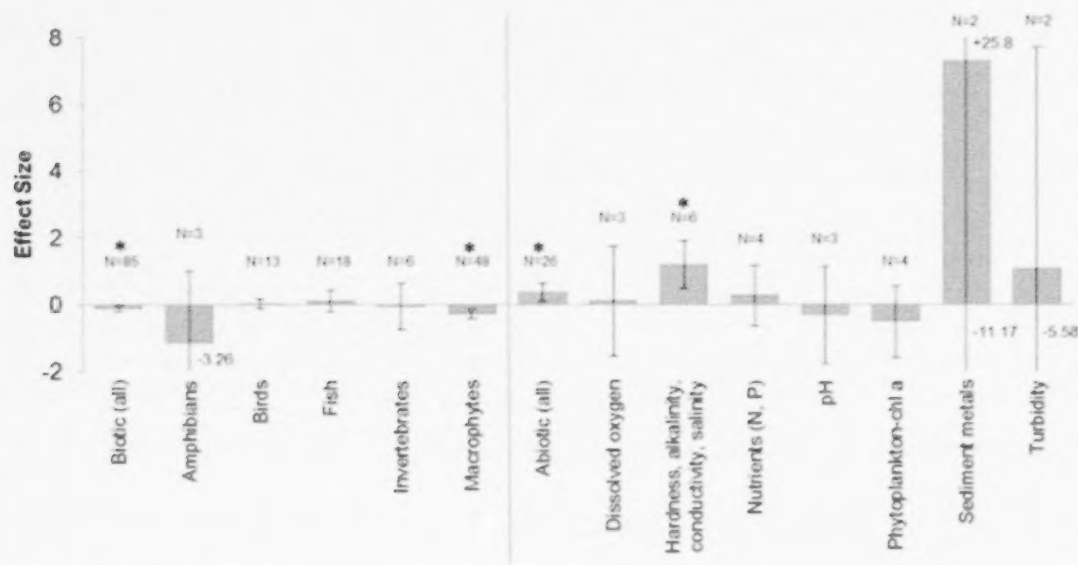


Figure 11. Results from meta-analysis on the impacts of Grass Carp on abiotic and biotic variables. 95% confidence intervals shown. *denotes a significant difference from 0. Figure developed using data from Table 1 in Wittmann et al. (2014).

In two review studies, the effects of alien invasive fish species were examined on a country scale. In Algeria, the introduction of Grass Carp into Obuira Lake led to the eradication of beds of submerged vegetation and reedbeds as well as increased turbidity, which has been linked to subsequent negative effects on the fish population and on wintering ducks using the lake (Kara 2012). A second lake, Pamvotis Lake in Greece, showed two clear effects: a decrease in submerged macrophytes; and, near disappearance of endemic and autochthonous cyprinids through competition, egg predation, and loss of habitat (Kara 2012). In Poland, several lakes have reduced fishing of Pikeperch (*Sander lucioperca*), Northern Pike (*Esox lucius*), Tench (*Tinca tinca*), Common Bream (*Abramis brama*), Roach (*Rutilus rutilus*), White Bream (*Abramis bjoerkna*), and European Perch (*Perca fluviatilis*) following Grass Carp introduction, as well as the depletion of wild fowl fauna, particularly those feeding on soft aquatic vegetation (e.g., the coot *Fulica atra*, and swans *Cygnus* sp.) (Grabowska et al. 2010).

Grass Carp is also believed to impact waterfowl by reducing aquatic vegetation, an essential food source and potential nesting habitat (GISD 2014). Significant declines of Gadwall (*Anas strepera*), American Wigeon (*Anas americana*), and American Coot (*Fulica americana*) have been reported following Grass Carp introductions (GISD 2014). Grass Carp may also affect amphibians; in one experiment, the abundance of Cricket Frog (*Acris crepitans*) was reduced in the presence of Grass Carp (Ade et al. 2010).

IMPACTS ON AQUATIC MACROPHYTES

Numerous studies have been carried out on the effect of Grass Carp on aquatic macrophytes, as it is extensively stocked for the control of aquatic macrophytes. The majority of these studies reported the stocking intensity and the success of aquatic macrophyte reduction or removal. For example, In New Zealand, Grass Carp stocked (40–80 kg/ha) in a canal dominated by coontail (*Ceratophyllum* sp.), or hornwort (*Ceratophyllum demersum* L.), reduced aquatic macrophyte abundance within 7 months by about 80% (Hicks et al. 2006). In a Saudi drainage, Grass Carp fingerlings (1–5 fish/m²) completely eliminated filamentous algae within 5 months and

significantly reduced the abundance of *Phragmites australis* (Belal 2007). In a small pond in the Czech Republic, stocked Grass Carp (29 kg/ha) reduced the biomass of aquatic macrophytes from 109 g/m² to 33 g/m² in one growing season (Pípalová et al. 2009). Grass Carp significantly decreased the biomass of *Cladophora globulina* Kutz., *Eleocharis acicularis* L., and *Potamogeton pusillus* L. The most preferred plant was the filamentous alga *Cladophora globulina*, the biomass of which decreased from 66 g/m to 0.4 g/m in the pond stocked with Grass Carp (Pípalová et al. 2009). Grass Carp has also been shown to be successful at suppressing the growth or eradicating Water Hyacinth (*Eichhornia crassipes*) (Gopalakrishnan et al. 2011). In earthen ponds in Turkey, Grass Carp was experimentally stocked for macrophyte control and *Cladophora* and *Zygnema* species of aquatic plants were consumed and eliminated within about a month, and *Chara* was eliminated within three months after stocking; overall plant biomass was 2.5 times lower in ponds stocked with Grass Carp (Kirkagac and Demir 2004). In this study, all vegetation except *Phragmites australis* was eliminated. In Dianchi Lake (China), the loss of *Ottelia acuminata*, a dominant macrophyte, was likely caused by the massive introduction of Grass Carp (Yang et al. 2013b). Kapuscinski et al. (2015) estimated Grass Carp populations could consume 96 mt of macrophytes in Buffalo Harbor and 4,941 mt in the upper Niagara River if they were to reach equal biomass to invasive Rudd (*Scardinius erythrophthalmus*).

Grass Carp can also influence the macrophyte composition through selective feeding. Krupska et al. (2012) reported changes in the composition of charophyte communities following Grass Carp introduction to a lake in western Poland, as well as a general decline in the number of aquatic macrophytes species. In an earthen pond (GA, U.S.) stocked with >100,000 juvenile, triploid Grass Carp, selective feeding by Grass Carp eliminated most palatable plants from the community and promoted the persistence of the chemically defended and unpalatable *Micranthemum umbrosum* (Parker et al. 2006). In Arkansas, following Grass Carp stocking for Hydrilla control, the macrophyte community shifted from American Lotus (*Nelumbo lutea*), Hydrilla, *Egeria*, Coontail (*Ceratophyllum* sp.), and Duckweed (*Lemnaceae* sp.), in descending order of dominance, to a community of American Lotus, Fragrant Water Lily (*Nymphaea odorata*), Coontail, Duckweed, and Hydrilla, in descending order of dominance (Timmons 2012).

IMPACTS ON WATER QUALITY

Grass Carp is often reported to affect water quality indirectly through the removal of macrophytes; however, the direction of change for different abiotic factors often varies across studies (Cudmore and Mandrak 2004).

Following removal of aquatic macrophytes, dissolved oxygen, carbon dioxide, turbidity, conductivity, and total dissolved solids increased (Belal 2007). In a southeastern U.S. reservoir, Grass Carp was intensively stocked to control Parrot-feather (*Myriophyllum aquaticum*) at a density of 100 fish per vegetated hectare, and post-stocking increases in ambient water chlorophyll *a*, reactive phosphorous, and nitrate-nitrite concentrations were recorded (Garner et al. 2008). In a small pond, stocked Grass Carp reduced aquatic macrophytes, which was associated with a decrease in the pH and nitrate-nitrogen concentration (Pípalová et al. 2009). In earthen ponds in Turkey, Grass Carp were stocked for macrophyte control and nitrite-nitrogen, nitrate-nitrogen, and total phosphate were higher in stocked ponds compared to ponds without Grass Carp (Kirkagac and Demir 2004). In a 10-week mesocosm experiment, Grass Carp significantly reduced macrophyte biomass through consumption and affected water quality, resulting in lowered pH and increased N-NH₄ concentrations (Dorenbosch and Bakker 2011). In Lake Warniak (northeastern Poland), rapid eutrophication occurred after the introduction of Grass Carp, which was followed by a decrease in clarity and a small increase in total phosphorus levels (Hutorowicz and Dziedzic 2008). Krupska et al. (2012) also reported a

reduction in water clarity following stocking of Grass Carp. By contrast, in Lake Conroe (Texas), triploid Grass Carp were stocked for Hydrilla control and, while there was an almost complete elimination of all aquatic plants, there were no clear changes in water quality parameters except for a significant increase in nitrate (Ireland 2010).

IMPACTS ON PLANKTON

In general, the effect of Grass Carp on plankton is inconsistent and depends on factors such as stocking density, season, and environmental conditions (Cudmore and Madrak 2004, Pípalová 2006). In earthen ponds in Turkey, Grass Carp was stocked for macrophyte control and subsequent sampling indicated that values of phytoplankton and zooplankton abundance were highest in ponds with Grass Carp compared to control ponds without Grass Carp (Kirkagac and Demir 2004). In an experiment assessing the ability of Grass Carp to process Duckweed (*Spirodela polyrhiza*), biomass of phytoplankton, dominated by filamentous and blue-green algae, was found to increase proportionately with the stocking density of Grass Carp (Pípalová 2003).

IMPACTS ON MACROINVERTEBRATES

In general, Grass Carp may affect macroinvertebrates through predation and through removal of macrophytes, which leads to loss of habitat for these organisms (Cudmore and Mandrak 2004). In New Zealand, canals stocked with Grass Carp were assumed to have a decrease in macroinvertebrates associated with macrophytes because the plants were completely removed, although this was not explicitly tested (Hicks et al. 2006). In Lake Tutira (New Zealand), following stocking of Grass Carp for Hydrilla control, macroinvertebrate diversity was maintained, but the relative abundance of taxa changed (Hofstra and Clayton 2014).

IMPACTS ON FISHES

Impacts to fish from Grass Carp introductions are varied, and the mechanisms are often not assessed (Dibble and Kovalenko 2009).

In Lake Conroe (Texas), changes in length-frequency and condition of centrarchid species, Largemouth Bass (*Micropterus salmoides*) diet changes, and changes in the fish assemblage among sampling stations was assessed before and after Grass Carp stocking (Ireland 2010). The diet of adult Largemouth Bass changed as it consumed less sunfish and more shad post-carp introduction, which is consistent with expected results from removal of vegetation eliminating small sunfish habitat. The length-frequency of centrarchids changed, as there were fewer juveniles; and, Gizzard Shad (*Dorosoma cepedianum*) significantly decreased in size following Grass Carp stocking (Ireland 2012). In a study conducted in Arkansas following stocking of Grass Carp for Hydrilla control, Bluegill (*Lepomis macrochirus*) and Largemouth Bass catch per unit effort (CPUE) moderately increased, but a causal mechanism was not discerned (Timmons 2012).

In New Zealand, diploid Grass Carp were introduced into a drainage canal at an initial density of 40–80 kg/ha (Hicks et al. 2006). Brown Bullhead (*Ameiurus nebulosus*) and Short finned eels (*Anguilla australis*) dominated the resident fish biomass in the canal and there was no observed change to the resident fish assemblage following Grass Carp stocking. However, young-of-the-year bullhead had greater mortality and grew faster in the canal with Grass Carp than in the canal without Grass Carp (Hicks et al. 2006).

In Asia, Grass Carp translocated to Donghy Lake, China, resulted in the reduction of submerged macrophytes and a subsequent upsurge of Bighead and Silver carps along with the disappearance of about 60 fish species (De Silva et al. 2009). Jiang et al. (2009) indicated that,

in the Chinese Lake Dianchi and White Dragon spring at Chenggong, Kunming (which flows into Lake Dianchi), a native cobitid fish known as Yi Se Yun Nan Qiu (*Yunnanilus discoloris*) is now endangered. The presence of invasive Grass, Bighead, Silver, and Black carps has negatively affected this fish.

Negative effects on native fish species can also be exerted by Grass Carp through the transmission of harmful parasites. For example, a number of *Dactylogyrus* spp. have been introduced to Iran with Grass Carp (Shamsi et al. 2009). It is unknown to what extent these species could jump hosts, but, as most native species in Iran are also cyprinids, the possibility cannot be ruled out (Shamsi et al. 2009). In the Czech Republic, the introduction of Grass Carp was accompanied by the introduction of the tapeworm species *Bothriocephalus gowkongensis*, which subsequently caused considerable losses in Common Carp cultures (Lusk et al. 2010).

IMPACTS ON HUMANS

Numerous studies, particularly in China, have identified the accumulation of metals in the tissues of Grass Carp, which may represent a potential food safety issue as the reported values exceed the guidelines for human consumption (Liu et al. 2012, Zhuang et al. 2013). In Turkey, the concentration of heavy metals in water and fish tissues of 3-year-old Grass Carp were above the maximum permissible level for human consumption (Yigit and Altindag 2006). In China, levels of organochlorine pesticides in Grass Carp tissue remain of concern, as the levels of bioaccumulation were considered substantial, particularly given human exposure over time in this area (Shi et al. 2006).

Laribacter hongkongensis is a recently discovered bacterium associated with gastroenteritis and traveler's diarrhoea and has been found in the intestines of Grass Carp from markets in Hong Kong and Guangzhou in southern China (Lau et al. 2007, Feng et al. 2012).

Cultured Grass Carp for consumption also represents a potential risk to public health due to infection by fish-borne zoonotic trematodes such as the liver fluke and intestinal flukes (Chi et al. 2008, De et al. 2012). In Vietnam, an estimated 1 million people are infected with such flukes, 1.5 million people in Korea, 6 million people in China, and over 5 million in Thailand (Chi et al. 2008).

Grass Carp has also been responsible for human death (Lam et al. 2004, Karatas 2010). The consumption of raw gallbladders of Grass Carp is used as a folk remedy in Asian countries (particularly China), which can result in acute renal failure and hepatitis due to the toxicity (nephrotoxicity) of Grass Carp bile (Chen and Huang 2013, Asakawa and Noguchi 2014).

HUMAN USE

Asian carps are used worldwide by the food industry. Grass, Bighead, Silver, and Black carps have been in aquaculture in China for at least one thousand years, since the Tang Dynasty (FAO 2015). People commonly captured larvae and raised them in ponds. More recently, artificial spawning has become a routine practice and significant efforts have been devoted to research on successful rearing practices to maximize production (FAO 2015). For example, numerous diet studies of cultured Grass Carp have been conducted to identify the diet that maximizes Grass Carp growth (see section 'Age and Growth'). A growing demand to use biological feed and not synthetic feed in aquaculture may represent a potential pathway for new aquatic invasive plants (Majhi et al. 2006).

Grass Carp is one of the most important freshwater fishes in China from an economic perspective (Yi et al. 2006) and, has typically been marketed fresh, either as whole fish or in

pieces. After Silver Carp, Grass Carp currently has the largest production in freshwater aquaculture globally although, in recent years, Grass Carp production has decreased in China due to interest in other species and changes in consumer preferences (FAO 2015). Outside of China, there has been rapid expansion of Grass Carp culture given its fast growth rate, large size, lack of fine inter-muscular bones, and feeding habits, which make the fish an ideal species for culture in developing countries (FAO 2015). The global aquaculture production of Grass Carp in 2002 is listed at a global value of USD 2.92 billion and, in 2012, 5.03 million tonnes of Grass Carp were produced (FAO 2015).

Most of the world's freshwater fish production comes from rural aquaculture via carp polyculture systems (e.g., Nguyen et al. 2005, Bolognesi da Silva et al. 2006, Barcellos et al. 2012, Hernández et al. 2014). During the grow-out of Grass Carp, polyculture with other species (e.g., Silver Carp, Bighead Carp, Common Carp, Mrigal, Nile Tilapia, and Rohu) is common practice, with Grass Carp often accounting for 60% of the total stocking density (FAO 2015). In China, there are about 85,000 reservoirs usually stocked with a carp polyculture system (Shelton and Rothbard 2006).

Grass Carp is also extensively used as a means of biocontrol for aquatic vegetation (Pípalová 2006). For example, Grass Carp has been used to control (*Hydrilla verticillata*), Peruvian Watergrass (*Luziola peruviana*), Hornwort (*Ceratophyllum demersum*), *Egeria najas*, and *E. densa* (Wells et al. 2003, Kirk and Henderson 2006, Stich et al. 2013, Manuel et al. 2013, Silva et al. 2014). Grass Carp has been extensively stocked worldwide with the intent to reduce aquatic vegetation and the use of herbicides in aquatic systems (Table 1). Grass Carp is one of the top ten fish species most often introduced or transferred (Froese and Pauly 2015). In 2000, an estimated 1 million Grass Carp (usually around 4–6 cm fingerlings) were stocked for weed control and valued at USD 3 million to U.S. producers (Shelton and Rothbard 2006). Grass Carp may also be used to help control snails by exposing snails (through removal of macrophytes) to predation by Black Carp (el-Deeb and Ismail 2007), and have been evaluated for their use as a biocontrol agent for larvae of anopheline mosquitoes (Ghosh et al. 2005).

Once Grass Carp is introduced, it is difficult to eliminate. Historically, managers have experimented with several methods for removing Grass Carp from lake systems, including herding, angling, attracting, use of lift nets, and toxic fish baits (Cassani et al. 2008). Unfortunately, all techniques used in the removal studies were time consuming, labour intensive, sometimes quite expensive and, in each case, failed to remove a major portion of the carp population. A newer method for the removal of Grass Carp from lake systems is the use of biodegradable capsules containing a fish toxicant that could be implanted in the carp and used to euthanize the fish after a given period of time (Thomas 2006). These, and other new methods for manipulating carp densities, could make the Grass Carp a more useful and acceptable aquatic plant management tool.

In the United States, concern over possible natural reproduction in introduced habitats has led to the development and use of sterile triploid Grass Carp for aquatic weed control with smaller numbers of diploid Grass Carp maintained in closed polyculture or monoculture pond systems (Pípalová 2006). Triploidy has been induced in Grass Carp in the U.S. for the purpose of preventing reproduction by stocked fish since the early 1980s (Mitchell and Kelly 2006). The USFWS also implemented a voluntary program, the National Triploid Grass Carp Inspection and Certification Program (NTGCICP), which certifies triploidy for stocking, thereby providing an impartial means of ensuring a low incidence of diploidy (USGS 2015). In the last 10 years, the program has certified almost 5 million triploid Grass Carp for nine producers (MICRA 2015).

While most states now require the use of triploid Grass Carp for vegetation control (Zajicek et al. 2011), regulations for Grass Carp trade (stocking, producing, certifying, and shipping) are

inconsistent across states (MICRA 2015). Based on 2013 regulations, 30.5 of 50 states allowed triploid Grass Carp stockings for biological control of nuisance aquatic vegetation, 7.5 states allow diploid stockings, and 12 states prohibit Grass Carp altogether. Numerous diploid Grass Carp suppliers (i.e., producers and/or distributors) exist: Alabama (16), Arkansas (36), Iowa (12), Mississippi (11), Missouri (13), and Nebraska (26); and, there are 9 commercial triploid Grass Carp producers located in five different states (Arkansas, Illinois, Alabama, Georgia, and S. Carolina) that participate in the NTGCICP (MICRA 2015).

Commercial harvest records of Grass Carp in the U.S. are difficult to obtain, but Grass Carp have been caught by commercial fisherman in Minnesota since the early 1990s. Captures were sparse until 2008 when flooding occurred, and totals caught in the Mississippi River in 2009, 2011, and 2012 were 254.9, 4.5, and 26.8 kg, respectively (MICRA 2015). From 1991 to 2007 and in 2011, data from the Wisconsin portion of the Mississippi River reported ≤ 136 kg of Grass Carp, but this value increased to an average of ~ 907 kg from 2008 to 2010 (MICRA 2015). Grass Carp caught by commercial fishermen in Illinois rivers between 2003 and 2011 ranged from 0 to 116,474 kg and, in Iowa, a total of 21,302 kilograms of Grass Carp was reported from 9 of 11 Mississippi pools (MICRA 2015). Based on annual landing query results from all U.S. states from 2003 to 2013 (only Louisiana has reported commercial harvest), an average of 42,426 kg of Grass Carp were captured annually (NOAA 2015).

Grass Carp was previously available in live fish food trade for markets in Canada. Prior to implementation of Asian carp regulations in Ontario in 2004 and 2005, it was reported that as much as 140,000 kg of Grass Carp was being sold by retailers in the Greater Toronto Area, with the majority coming from the U.S. aquaculture or commercial fisheries (Goodchild unubl. rep.). Between 2002 and 2003, live fish markets located in close proximity to lakes Erie and Ontario were visited and, in three of the six markets, Grass Carp were available for purchase (Rixon et al. 2005).

CONSERVATION STATUS AND REGULATION

Grass Carp has not been evaluated by the International Union for the Conservation of Nature (IUCN) but, in 1996 was listed as globally secure (i.e., at very low risk of extinction or elimination due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats) by NatureServe (2015). A national, state, or provincial conservation status of NNA or SNA (not applicable) was assigned in 1996 for the United States and Canada, indicating that the species is considered not a suitable target for conservation activities because it is a non-native species in these countries (NatureServe 2015). A United States Invasive Species Impact Rank has not yet been assessed for Grass Carp (NatureServe 2015); however, it has been listed as a potential pest species (Froese and Pauly 2015) and is listed on the Great Lakes Aquatic Nonindigenous Species Information (GLANSIS) watchlist (i.e., not currently found in the Great Lakes but assessed in the peer-reviewed literature as of 2010 as likely to invade via current pathways) (GLANSIS 2014).

Unlike the Silver and Bighead carps, Grass Carp is not listed as injurious wildlife under the *Lacey Act* in the United States (USDA 2013). The *Lacey Act* gives jurisdiction to the United States Fish and Wildlife Service to ban the import and transport of species listed as injurious wildlife. The most protective regulatory approach for Grass Carp would be for all states to prohibit both diploid and triploid Grass Carp; however, Grass Carp has multiple commercial applications and considerable economic value in some states (MICRA 2015). This has resulted in a mosaic of Grass Carp state regulations regarding importation, possession, and stocking. Disparate Grass Carp regulations also exist in Canada (Table 4); however, Fisheries and Oceans Canada worked with other federal and provincial agencies towards a uniform approach

and now has national regulations for aquatic invasive species in force (as of June 2015), including for Asian carps.

Table 4. Summary of Canadian provincial and territorial regulations pertaining specifically to the import, trade, possession, or stocking of Grass Carp (Ctenopharyngodon idella). General regulations pertaining to fish possession are listed below species-specific regulations. Regulations are categorized as either not restricted (i.e., no permit required, not prohibited), restricted (i.e., permit required or limited use), or prohibited by Provinces and Territories. (DFO, unpubl. data).*

Province/Territory	Summary of Provincial/Territorial Regulations for Grass Carp
Alberta	Diploid Grass Carp are not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) Triploid Grass Carp are restricted (i.e., permit required to import, trade, possess, and stock for aquaculture purposes; private license holders can buy but not traffic or sell triploid Grass Carp and live specimens may not be transported from licensed private ponds after stocking. Only triploid Grass Carp may be stocked.)
British Columbia	Prohibited (i.e., no person shall import, possess or trade live specimens of these species.)
Manitoba	Prohibited (i.e., no person shall import, possess, transport or release into any waters live specimens or live eggs of these species. Specialized authorization to import and possess specified quantities of live specimens for qualified scientific research purposes may be attained from the provincial Minister.)
New Brunswick	Not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) General: No person shall use as bait or possess for use as bait, live or dead goldfish or other carp.
Newfoundland and Labrador	Not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) General: No person shall import or bring into the province any wild animal (i.e., any live animal, including without limitation, any fish, whether or not bred, hatched or born in captivity and including any egg or offspring of them).
Nova Scotia	Not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) General: possession of live fish is prohibited except if a person has a license or written permission, or if the fish is intended for live bait, private aquarium, catch and release, or for stocking or educational purposes.
Ontario	Prohibited (i.e., no person shall import, buy, sell, possess or use for aquaculture live specimens or viable eggs of these species. Specialized authorization may be granted by the provincial minister for qualified scientific research in a recognized research facility. Dead carp are not prohibited.)
Prince Edward Island	Not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) General: No person shall use as bait or possess for use as bait, live or dead goldfish or other carp.
Quebec	Prohibited (i.e., aquarium, fish-keeping, production, keeping in captivity, breeding,

Province/Territory	Summary of Provincial/Territorial Regulations for Grass Carp
	stocking, transport, sale, or purchase as live fish is prohibited.)
Saskatchewan	Not restricted (i.e., no regulations or restrictions pertaining specifically to these species.) General: No person shall use as bait or possess for use as bait, any live fish. No person shall obtain, transport, or possess any live fish of any species without an aquaculture license.

In contrast to North America, conservation of Grass Carp throughout their native range is of increasing concern to government agencies tasked with the protection of fisheries (Duan et al. 2009). Grass Carp represents one of the four most economically important fishes in China and its abundance has declined in many areas (Jiang et al. 2010). The Yangtze River is the largest river in Asia and has the most abundant population of Grass Carp (Li et al. 2013); however, due to overfishing, water pollution, and hydrological modifications, there has been a major reduction in Grass Carp recruitment and a rapid decline in Grass Carp abundance (Xie et al. 2007, Zhao et al. 2011a). During the planning phase of the Gezhouba and the Three Gorges Dam on the Yangtze River, significant consideration was given to building structures that may exert a detrimental effect on Grass Carp spawning and migration (Chapman and Wang 2006). Despite these considerations, results indicate that harvest levels (2003–2005) of Bighead, Black, Grass, and Silver carps below the dams was 50–70% lower than pre-impoundment levels (2002) (Xie et al. 2007). Over this same time period, the abundance of drift-sampled carp eggs and larvae sampled below the dams declined by up to 95% (Xie et al. 2007).

Of all four economically important Asian Carp species, Grass Carp production was most significantly impacted (Duan et al. 2009). Before impoundment, Grass Carp was the most abundant of the four Asian carps, but the hydrological changes negatively affected the growth of aquatic macrophytes, and the proportion of Grass Carp subsequently declined (Jiang et al. 2010). Modified seasonal cues for migration and reproduction resulting in delayed spawning and suppressed growth may also explain the decline following impoundment (Xie et al. 2007, Zhang et al. 2012). Similar declines following hydrological modification have been documented in other rivers, such as the Pearl and Hangjiang (Li et al. 2008, Tan et al. 2010). Interestingly, sampling of drifting eggs and larvae in the upper Yangtze River suggests that Grass Carp have moved upstream and established new spawning sites, and this upper reach may represent an important area for future protection (Jiang et al. 2010). Given the migratory behaviour of Grass Carp, suggested conservation efforts included closing the fishing season during the breeding season; ecological regulation of dams; stocking, recovery, and reconstruction of spawning habitat; and improving connectivity between the river and its lakes (Fu et al. 2003, Duan et al. 2009, Chen et al. 2009b, Li et al. 2013, Ru and Liu 2013).

Due to declining fishery resources and the growing development of conservation aquaculture, the genetic diversity of native wild Grass Carp has also become an area of concern (Yang et al. 2013b). Artificial production and stocking of Grass Carp into the Yangtze River to improve fisheries and protection may cause lowered genetic diversity and genetic contamination; therefore, selection of strains with desirable characteristics is recommended (Chen et al. 2009b). Recent studies have examined the genetic diversity and variation of Grass Carp to understand impacts of hydrologic changes and to identify ways of conserving and/or improving genetic resources for wild and cultured Grass Carp populations (e.g., Zheng et al. 2007, Liu et al. 2009, Zhao et al. 2011a, Fu et al. 2013).

SUMMARY

Since the introduction of Grass Carp to the United States in the 1960s, this species has spread throughout the Mississippi River basin. Grass Carp have also been introduced to a number of other drainage basins in North America. The populations now established throughout major tributaries of the Mississippi River threaten to expand into the Great Lakes through connected waterways and other potential pathways. Recent captures of both diploid and triploid Grass Carp in the Great Lakes basin suggests stock contamination, migration of diploids through connected waterways, and/or presence of reproductively viable Grass Carp populations in the Great Lakes. Efforts continue to prevent introduction to the Great Lakes, including assessment of various mitigation options, the maintenance of an electric fish barrier system in the Chicago Sanitary and Ship Canal, intensive monitoring, and population control.

This biological synopsis was required to update current information on this aquatic invasive species, as the body of scientific literature has expanded substantially over recent years. It surveyed studies from 2003 to early 2015. As described in this report, Grass Carp is a long-lived species with a broad physiological tolerance. It has high fecundities and are voracious herbivores typically occupying large river basins. It is capable of migrating large distances and has been associated with negative impacts on a variety of taxa and foodwebs. This species is also used extensively by people worldwide for food and aquatic macrophyte control. Recent legislation in both Canada and the United States has begun to control human-mediated movements of Asian carps, including Grass Carp, to deter future introductions and spread.

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